INHERITANCE OF SOME COMPONENTS OF RESISTANCE TO EARLY LEAF SPOT CAUSED BY *CERCOSPORA ARACHIDICOLA* HORI. IN PEANUT (*ARACHIS HYPOGAEA* L.)

By

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Dedicated to my father, the late Mafinhwa Francis Mungati Chiteka, and my mother, Maria Rosa, for the selfless love of their family, dedication and the sacrifices that charted the course to this achievement.

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Early leaf spot, caused by *Cercospora arachidicola* Hori. (Ca), and late leaf spot, caused by *Cercosporidium personatum* [(Berk. and Curt.) Deighton] (Cp), are major foliar diseases that reduce peanut yields. Fungicides can be used for control but resistant cultivars are more sustainable, economical, and environmentally more desirable. Genotypes with varying levels of rate reducing components of resistance have been identified. Research was conducted to study the inheritance, stability, and consistency over seasons in two diverse environments, Florida and Zimbabwe, for four components of resistance to early leaf spot, namely, latent period (LP), lesion diameter (LD), amount of sporulation (SP), and maximum percentage sporulating lesions (MPSL). Four genotypes that varied in levels of resistance to Ca were used to make full diallel crosses including reciprocals. Two tetrafoliate

leaves from randomly selected plants from each cross, totalling 10, 30, and 72 for F_1, F_2, and F_3, generations, respectively, were inoculated with conidia of local strains of Ca. Analyses of variance, regression, combining ability and correlation analyses were computed. Narrow sense heritability estimates significantly different from zero were obtained for each component and estimates varied from 0.0 to 0.64 for LP, 0.0 to 0.45 for LD, 0.0 to 1.27 for SP and 0.0 to 1.20 for MPSL. The ratio of mean squares for general combining ability (GCA) to specific combining ability (SCA) ranged from 5 to 12 for LP, 2 to 3 for LD, 4 to 21 for SP and 7 to 34 for MPSL. Resistance to Ca is controlled by additive genes, therefore selection within crosses in early generations could be an effective strategy in breeding for resistance to Ca. Reciprocal effects were noted for some crosses, indicating that cytoplasmic factors could be involved in the inheritance of resistance. Latent period was negatively correlated ($P \leq 0.05$) with SP and MPSL in most tests ($|r|=0.251$ to 0.666). Amount of sporulation was positively and highly correlated ($P \leq 0.05$) with MPSL ($r=0.500$ to 0.824). Selection for long LP may also reduce SP and MPSL. Latent period, SP, and MPSL were consistent components in evaluating genotypes for resistance to Ca but LD was not. Correlations between measurements of components between Florida and Zimbabwe were low and mostly not significant. Genotypes that are resistant to Ca in Florida may not be useful in Zimbabwe.

CHAPTER I
INTRODUCTION

Peanut, (*Arachis hypogaea* L.) originated in Latin America (47, 50) and the genus *Arachis* has a diverse group of diploid and tetraploid taxa that are native only to South America. This genus is found in the area ranging in latitude from near the mouth of the Amazon river to 34°S to the northern bank of the Rio de la Plata river in Uruguay, extending westward from the Atlantic to the eastern foothills of the Andes between 35 and 66°W longitude. To the north, it is bound by the southern border of the Amazonian Forest. It is believed that the center of distribution of the genus *Arachis* is the Brazilian Planato Ellipse (47, 72).

Peanut is now grown all over the world, between latitudes 40°N and 40°S. The peanut is rich source of vegetable oil, which ranges from 42 to 53.6% in the cultivars (102) and 46.5-63.1% in wild species (93). Peanut ranks fourth in the world as a source of vegetable oil and the third, as a source of vegetable protein. Presently, 40% of world crop is processed into oil, which is used for domestic and industrial purposes (8). Peanut is an important human food legume crop that can be consumed fresh when roasted or cooked. The dry seed is

processed into peanut butter and various confectionery products. In many developing countries, staple diets are based principally on one or more of such crops as cassava, corn, sorghum, millets, rice and others. They are typically high in carbohydrates and low in protein. Crude protein in peanut seed ranges from 25 to 30% in cultivars (67) and thus makes an important supplement to high carbohydrate, protein deficient staple diets (102).

In most of the peanut producing countries, the crop is produced by small scale subsistence farmers under low input conditions and yields range from 400 to 1000 $kgha^{-1}$ (31). Among the main reasons for the low mean yields achieved in these countries are the use of unadapted, low yielding cultivars, low rainfall, often with mid season drought stress, diseases and insect pests (92).

Two of the most important diseases affecting peanut are leaf spot diseases are early leaf spot caused by *Cercospora arachidicola* Hori. (Ca) and late leaf spot caused by *Cercosporidium personatum* [(Berk. and Curt.) Deighton] (Cp). These affect peanut wherever the crop is grown (61, 92, 83). Yield losses due to leaf spot diseases are estimated at 10 to $\geq$ 50% (108, 117).

Leaf spot diseases can be successfully controlled using available fungicides (41, 108, 116, 118). In developing countries, fungicides are either unavailable or uneconomical (92, 105). In addition, the application of fungicides poses

health hazards to humans and has undesirable environmental effects (106, 118). The use of resistant cultivars is a highly sustainable, long term strategy for the control of leaf spot diseases.

Genotypes with resistance to Ca have been identified (1, 105, 135). There are no sources of single gene immunity to Ca in *A. hypogaea* (105). However, some wild species have been reported to be immune to Ca (128). These sources are not readily available for use because the wild species are diploid while the cultivated peanut is tetraploid.

The type of resistance to Ca reported in cultivated peanut was found to be partial or incomplete (100, 105, 136). Partial resistance to Ca has been attributed to a variety of components that work together to reduce the rate of disease progress in a peanut crop (65, 88, 128, 135). Peanut genotypes, NC 5, NC 3033, and NC-GP 343, with moderate levels of resistance to Ca, were released in North Carolina (71). These have, been found to be susceptible to Ca in Malawi and in India (92). In Florida, a high yielding peanut cultivar with partial resistance to Cp, Southern Runner, was released (40). Several other genotypes with resistance to Cp equal to or higher than Southern Runner and with yield equal to or better than Southern Runner have also been reported (43, 95, 108).

To develop cultivars with resistance to Ca and Cp it is necessary to understand the nature and inheritance of

resistance to formulate the best breeding strategy. Higgins (54) concluded that resistance to the two leaf spot diseases is inherited independently and work by Anderson et. al. (4) supports this conclusion. The various components of resistance may be under the control of different genes (5, 138). It should therefore be possible to combine different components of resistance and achieve greater resistance in one cultivar. The inheritance of resistance to Ca is still not clearly understood.

CHAPTER II
LITERATURE REVIEW

Introduction

Leaf spot diseases are among the major diseases affecting peanut wherever it is grown (35, 80, 116, 118). Early leaf spot is caused by *Cercospora arachidicola* Hori (Ca) (teleomorph *Mycosphaerella arachidis* Deighton). The anamorph of the late leaf spot pathogen has been known as *Cercosporidium personatum* (Cp), but Von Arx (132) proposed the change to *Phaeoisariopsis personatum*. The teliomorph of Cp is *Mycosphaerella berkeleyii* W. A. Jenkins. These pathogens are exclusive to the genus *Arachis*. The two pathogens reduce yields by 10 to >50% under unsprayed conditions (80, 116). The two leaf spot diseases often occur together, but early leaf spot usually occurs earlier in the growing season than late leaf spot. In the USA, Ca is more prevalent in Virginia, North Carolina, Oklahoma, and New Mexico. Cp has been generally more predominant in Florida, Georgia, and Alabama since the late 1970s, but both can occur together (94). The prevalence of one or the other depends on cultivar, environmental conditions and management of peanut crops in a region (94, 118). In 1992, Ca remained predominant throughout the season in many parts of Georgia and Alabama.

Early Leaf Spot (Ca)

Lesions of Ca may be formed on leaves, petioles, stems and pegs. Lesions are circular, or irregularly shaped, being up to 10 mm in diameter but may coalesce to form larger lesions, especially over a major leaflet vein (83). Early leafspot lesions are medium brown to black in color on the upper surface and may or may not be surrounded by a chlorotic yellow halo, depending on environment and cultivar (80). Conidiophore production is sparse, randomly distributed, and occurs predominantly on the upper leaf surface. Early leaf spot has a lighter color on the lower leaf surface than late leaf spot. These characteristics are used to distinguish Ca from Cp but microscopic examination of lesions of Ca reveals features that separate it from Cp more clearly. Lesions of Ca produce subhyaline olivaceous conidia 35-110 µm and are much more slender than conidia of Cp. Conidia of Cp are 20-70 µm x 4-9 µm and have a finely roughened wall (86). Conidia are the principal source of inoculum that propagate the two pathogens. Infection is favored by temperatures of 25-30°C with high relative humidity (80, 116).

The leaf spot pathogens survive in crop debris from previously infected crops (83, 94, 118). Seed transmission is not important, accounting only for surface infestation with conidia (80). The conidia are spread by wind or rain splash from plant to plant.

The anamorph of Ca typically has stromata up to 100 µm in diameter, slight to dark brown in color (83). Conidiophores are arranged in dense fascicles, five to many in number, pale olivaceous or yellowish in color and darker at the base of the leaf, mostly once geniculate, unbranched, 15-45 x 3-6 µm in size. Conidia are subhyaline slightly olivaceous obclavate, often curved, 3-12 septate with base rounded to truncate, tip sub-acute 35-110 x 0-5.4 µm in size.

Conidia of Ca germinate to form one to several germ tubes which grow on the leaf surface, and penetrate open stomata, but direct penetration has also been observed. The early leaf spot fungus kills cells in advance of the proliferating hyphae while Cp produces botryose haustoria, and does not kill cells in advance of proliferating hyphae. Germination and germ tube elongation of Ca was found to be best at 19-25°C but was low at 28-32°C with night temperatures of 19-25°C favoring germination (2). Sporulation of *C. arachidicola* on leaflets incubated at 100% R.H. was greatest at 24-28°C, intermediate at 20°C and least at 16 and 32°C (2). Early infections often begin on lower leaves near the soil surface and the epidemic proceeds upwards until defoliation occurs (83).

Effects of Leaf Spot Diseases on Peanut

Leaf spot diseases affect the leaves, petioles, stems and pegs of the plant (52, 63). The two together may cause 5 to > 50 yield loss or more (79, 108, 116, 117). Yield reductions

of 70% have been reported in India (127), and yield losses of 80% have been observed in experimental plots in the USA (68, 76). Bunting et al. (1980) cited by Smith et al. (118), estimated world losses at 3 million metric tons per year as a result of leaf spot epidemics. Peanut leaves infected with Ca produce ethylene which induces defoliation (66). No defoliation was found on a plant introduction that produced only background levels of ethylene. Leaf spot diseases cause premature defoliation, reducing the total photosynthetic area available, and hence reducing yield (11). Peanut leaves contain a much higher percentage of protein than stems and branches, consequently defoliation reduces both the yield and quality of hay from a peanut crop (27, 79). In addition, defoliation weakens the pegs and results in a loss of pods that have already been formed (68). Defoliation provides a substrate that can encourage the growth of *Sclerotium rolfsii* which causes southern stem rot of peanut (117).

Bourgeois and Boote (11) showed that photosynthesis in leaflets infected with Cp decreased linearly with increase in percent necrotic area. A 15% leaf necrotic area contributed to a 65% reduction in photosynthesis of infected leaflets. They showed that defoliation was more important in reducing canopy photosynthesis than the reduction in leaflet photosynthesis.

Control of Leaf Spot Diseases

A variety of management strategies can be employed to control leaf spot diseases in an integrated pest management system. An integrated system for management of peanut leaf spot diseases has been described by Shokes and Smith (107). The management of leaf spot diseases generally involves the adoption of specific cultural practices, use of fungicides, biological control, and the use of resistant cultivars.

Cultural Practices

Cultural practices like crop rotation, burial of crop residues variation of the planting date and avoidance of environments conducive to disease help control Ca (94, 118). Crop rotation delays the onset of disease and reduces the rate of disease progress (73). Burial of crop residues reduces the amount of initial inoculum, while variation of planting date may be used to avoid environmental conditions favorable for development of Ca. Other cultural practices such as fertility management, land preparation, and application of supplementary irrigation may affect disease progress and the level of disease control achieved (94, 118). However, these are inadequate to prevent losses, and fungicide use is necessary to maximize yields. In many developing countries, fungicides are not used due to the low yield potential of local cultivars, the high cost and difficulty of procuring fungicides, unavailability and high cost of application

equipment, low market value of the crop, and difficulties of obtaining and transporting good quality water to use for spraying (80).

Fungicides

Reports on the successful control of leaf spot diseases using fungicides are numerous (24, 71, 74, 75, 76, 94, 98, 110, 118). Although fungicides are very effective for the control of leaf spot diseases, they are expensive and may cause increases in non target pathogens (91). In the USA, the use of fungicides to control leaf spot diseases in peanuts is estimated at $32.7 million annually (106). This represents 16% of the production costs of peanuts in the USA (105).

In some peanut growing areas such as South Africa, Zimbabwe, and Texas, web blotch, caused by the *Phoma arachidicola*, is an important peanut foliar disease (118). Some fungicides (e. g. benomyl) are effective against Ca and Cp but not effective against web blotch (118). The use of benomyl to control leaf spot diseases resulted in an increase of web blotch in Zimbabwe (21).

Biological Control

Some fungi and bacteria have been reported to parasitize Ca, Cp, and rust on peanuts. The bacteria species *Bacillus thuringensis* and *Pseudomonas cepacia* PC 742 were reported to give excellent control of Ca under laboratory conditions

(122). The level of control with chlorothalonil foliar sprays was superior to the amount of control achieved by bacterial sprays. The fungal species *Verticillium lecanii* (*Hansfordia pulvinata*) was reported to parasitize Cp in India (36) and in Florida (109). In inoculation experiments, Subrahmanyam et al. (129) found a significant reduction in the extent of rust and late leaf spot development on peanut leaves inoculated with *V. lecanii* (Zimmerm.) Viegas. No quantitative differences in development of Ca in the presence of *V. lecanii* have been reported. No biological control agent has been reported to achieve the equivalent level of field control of Ca and Cp of fungicides.

Disease Resistance

Disease resistance is the most economical long term method of control and is environmentally more desirable. The use of disease resistant cultivars may eliminate the need for fungicide applications and avoid some of the undesirable effects on nontarget organisms. This should increase profitability of peanut production and increase farm income. However, few cultivars have been released for their resistance to Ca or Cp, despite breeding efforts for resistance in many programs (70, 92, 143).

Selection for high yield under disease pressure at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) resulted in the release of two *A. hypogaea*

lines ICG87160 and ICGV86590 which have moderate levels of resistance to foliar diseases (92). Several stable tetraploid interspecific derivatives with good yield but late maturity have also been identified (92, 95). The fodder quality of disease- resistant lines is better than susceptible cultivars due to the higher leaf retention. In the ICRISAT Malawi program, breeding lines with high yield under heavy disease pressure were identified (92). These lines retain a higher percentage of foliage for a longer time compared to susceptible cultivars.

In the USA, Southern Runner, a high yielding cultivar with partial resistance to Cp, has been released (40). The use of the partially resistant cultivar Southern Runner can reduce the number of fungicide sprays from eight to four during a growing season without significant yield loss in the southeastern USA (25, 94).

Breeding For Resistance

Sources of Resistance

Numerous sources of resistance to leaf spot diseases have been identified in different environments (1, 15, 34, 42, 51, 82, 91, 94, 130, 136, 141). Sources of resistance to Ca include NC3033, NC5, PI270806, GP-NC343, PI109839, PI259747, PI350680 (32, 46, 51, 121). At ICRISAT, 53 accessions of *A. hypogaea* identified to be resistant to Cp, and 29 of these

also have resistance to rust (92). The wild species from the section Arachis, *A. chacoense* (PI276325), *A. cardenasii* (PI262141) and *A. stenosperma* (PI338280) are immune to Cp and are cross compatible with *A. hypogaea*. From other sections, highly resistant wild species include *A. repens*, *A. appressipila*, and *A. glabrata*).

In the USA, a number of lines have epidemiological components of rate-reducing resistance to Ca. Some of these lines, NC3033, PI270806, PI259747 and PI350680, did not show resistance in India or in Malawi (92). In tests for resistance to Ca at ICRISAT, only 7 out of 3000 genotypes showed moderate levels of resistance to Ca. In Malawi, bulk testing was used to evaluate 11000 lines. Seed from ten lines were mixed to make 1100 bulk lots to represent the 11000 lines and the bulk lots screened for resistance to Ca in Malawi. Only three lines ICG 50, ICG 84, and ICG 11282, merited further testing. Thirty-five lines, reported to have resistance to Ca at ICRISAT Center were susceptible in Malawi (ICRISAT, 1989), according to Islieb et al. (60).

Of the various wild species reported to be resistant to Ca, only *Arachis* spp. 30003 has proved to be resistant in Malawi using the infector row technique. *A. stenosperma*, which was reported to be highly resistant to Ca in the USA, was found to be highly susceptible in Malawi.

Many of the resistant germplasm lines in *A. hypogaea* have thick walled pods that are hard to shell, are highly

reticulated, deeply constricted with prominent ridges, and conspicuous beaks. Many of these have an unattractive pod appearance that retains excessive soil on the pod surface.

When unadapted, resistant lines are crossed with adapted cultivars, the resulting resistant progeny identified were frequently of later maturity (143). The cultivar Southern Runner, with partial resistance to Cp, matures two weeks later than the cultivar Florunner. The latter is also one of the parents of Southern Runner (40). The late maturity presents problems in the semi-arid tropics where growing seasons are short, or when the crop is grown in multiple cropping systems.

More recently Cp-resistant genotypes with acceptable maturity have been identified. The Cp resistant genotype GA T-2844 is reported to mature 30 days earlier and yield 30% more than Southern Runner in unsprayed replicated tests over four seasons in Georgia (12).

Ouedraogo et al. (95) evaluated nineteen selected interspecific peanut lines with resistance to leaf spots for three years with and without spray. One line had values of the area under disease progress curve (AUDPC) equal to or lower than the partially resistant cultivar Southern Runner. Early leaf spot was predominant in all seasons tested.

Gorbet et al. (41) reported results from tests using sprayed versus unsprayed treatments on susceptible and partially resistant peanut genotypes. The spray treatments consisted of 14-day and 20-day intervals, using

chlorothalonil. There were significant differences among genotypes in the untreated tests and negative correlations between pod yields and disease ratings for the unsprayed and for the 20-day treatment but not for the 14-day treatment for resistant genotypes. No differences in pod yield were obtained between the 14-day (8 sprays) and the 20-day (4 sprays) fungicide treatments for resistant genotypes. Results from such tests showed that it is possible to develop acceptable peanut cultivars with resistance to Cp (41, 119).

Previous research has shown a negative association between high yield and resistance (67, 93). However partially resistant genotypes with high yields were identified (41, 95).

Disease assessment methods

A variety of disease assessment methods have been used to evaluate peanut genotypes for resistance to Ca and Cp. An ideal disease assessment method should be easy to use, provide a rapid, accurate, and reproducible estimate of disease intensity over a range of conditions (111, 118).

Resistance to Ca and Cp in *A. hypogaea* is partial. Components of resistance such as lesion number, latent period, sporulation, amount of diseased tissue, percent defoliation, and remaining green leaf tissue have been widely studied (118). Nevill and Evans (90) evaluated peanut genotypes for resistance to leaf spots using a general score. They noted that host development and pathogen effects could be confounded

during assessment, and proposed the use of single branches to make disease assessments.

Melouk and Banks (81) developed a detached leaf technique for evaluating genotypes for resistance. This method has the advantage that it is reproducible and requires a minimum amount of leaf tissue, space and fungal inoculum. This latter method has been used by various investigators (33, 87, 128, 135, 139). Results of greenhouse tests using this technique, however, do not always correlate well with field results.

Rating scales are commonly used in field assessment of resistance to leaf spot diseases. Two typical rating scales used are the International Crops Research Institute for the Semi Arid Tropics (ICRISAT) 1-9 scale (128) and the Florida 1-10 scale (14, 42). In these assessments, the stage of development of the crop should be specified. Boote (10) developed a growth stage key for peanut which can be used to define the ontogenic stage of the crop at the time of assessment.

Defoliation has been widely used in the evaluation of disease resistance and is included as a factor in field rating scales such as the ICRISAT 1-9 and the Florida 1-10 scales. Disease assessments using percent defoliation have been reported by numerous researchers (3, 42, 59, 85, 97, 98). Bourgeois and Boote (11) reported that the decrease in leaf area index due to defoliation was the major component involved in reduction in peanut canopy photosynthesis. They found that

canopy photosynthesis was inversely proportional to disease severity. Defoliation determines the amount of remaining healthy leaf area at a given time in the growth cycle of a crop and hence the healthy leaf area duration (HAD). Healthy leaf area has been determined using canopy reflectance techniques. Aquino et al. (7) reported that the pod yield of the cultivar Florunner was reasonably predicted by HAD and predicted yields were within 11% of the actual yield.

Greenhouse and field assessments

In screening genotypes for resistance to Ca, it would be desirable to screen large numbers of genotypes in the greenhouse in order to reduce costs. Only the most resistant genotypes identified would then be taken to the field for further testing. For this approach to be useful, genotype performance in the greenhouse should rank similar to that in the field.

Significant positive rank correlations between greenhouse and field evaluations for lesion area, latent period and number of lesions per 15 leaves for Ca have been reported by Walls et al. (13). Significant rank correlation between greenhouse and field ratings for amount of spore production, lesion diameter and latent period were reported for Cp (17, 15 128). Rank correlations between greenhouse and field ratings for percent leaf necrotic area determined, using a pictorial chart, were low for Cp (15).

Nature of Resistance

Breeding for resistance to foliar diseases in peanuts is a major objective in many peanut breeding programs (41, 60, 67, 70, 93, 143). It is essential to understand the nature of resistance in resistant genotypes since this may affect the breeding strategy (1, 143).

The breeding strategy used in developing resistance against monocyclic pathogens may be different from that employed for polycyclic pathogens that are both soil and air borne (143). Incidence and severity of disease depends on climatic conditions and this affects the screening methods and the breeding strategy.

Disease escape may result when a cultivar matures and produces economic yields during periods before or after major epidemics. This strategy has been effective with some monocyclic soilborne pathogens (19) but is of limited value with windborne pathogens like Ca and Cp.

Some resistant genotypes produce pectic substances and exhibit a thickening of the cell walls (1). A directed growth of germ tubes toward stomata was observed in susceptible cultivars, whereas no directed growth was observed on moderately resistant genotypes. Other characteristics positively correlated with resistance are riboflavin content of seed, thick palisade layer and small stomata.

Resistance to Ca has been reported to be associated with the production of phytoalexins upon infection. The principal

phytoalexin found in peanut leaves infected with Ca was identified to be medicarpin (124). Eleven other anti-fungal compounds were isolated from foliage infected with rust (125). Phytoalexins are assumed to inhibit pathogen ingress and/or reproduction in peanut tissues. Genotypes that produce high levels of phytoalexins were found to utilize more methionine rich protein than low phytoalexin producers (84).

Phenolic compounds have also been reported to inhibit the growth of Cp in vitro (131). These compounds enhance host resistance by stimulating host defense mechanisms (125). Peanut leaves infected with Ca were found to have a higher activity of 1,3-β-glucanase which was limited to infected tissue (101).

There are conflicting reports on the influence of stomatal aperture on resistance to Ca. Stomatal aperture has been reported to be correlated with field resistance to Ca in field grown *Arachis* species (38) while other studies reported that stomatal size is not a mechanism of resistance (22, 51).

Leaf area replacement and partitioning

Some alternate branching types of the sub-species hypogaea were reported to be more resistant to Ca than genotypes in the sub-species fastigiata (52). Alternate branching types are more proliferous leaf producers and may therefore appear to be relatively less infected than sequential types due to the dilution effect. The cultivar, Southern Runner, with moderate resistance to Cp (40), also has

physiological tolerance to Ca and Cp resulting from significant leaf production late in the season (118). This enables Southern Runner to tolerate defoliation and achieve high yields even under high disease pressure (98). This leaf area replacement potential may not be the optimum mechanism for minimizing the effects of leaf spot diseases because it uses up carbohydrates which could be used for pod filling to increase yield (11).

Duncan et al. (29) compared the crop growth rates, fruit growth rates, and partitioning of peanut cultivars released at different times in the Florida peanut breeding program in tests sprayed with fungicides for leaf spot disease control. They found no significant differences in crop growth rates for high yielding and low yielding cultivars. Breeding for high yield resulted in selection of genotypes with a high partitioning coefficient for photosynthate to reproductive growth. Partitioning ranged from 41% in low yielding cultivars to 98% for high yielding cultivars. Growth and partitioning interact with disease resistance. During the pod filling phase, the photosynthetic canopy is subject to defoliating agents such as foliar diseases, and leaf-eating insects which reduce the photosynthetic area available. Under leaf spot disease pressure, a cultivar with a higher leaf area replacement potential during the pod filling phase may be more desirable than one with a higher partitioning to fruit and no leaf area replacement potential during the same period. In

order to achieve high yields, the cultivar with a lower partitioning would require a longer pod filling period than one with a higher partitioning coefficient to achieve the same fruit yield. Pixley et al. (98) reported resistant genotypes UF81206 and MA72x94-12 with partitioning coefficients of 77% and 53%, respectively, compared to the susceptible cultivar Florunner with a partitioning coefficient of 92%. Knauft and Gorbet (69) showed that it is possible to combine a moderately high partitioning coefficient with disease resistance. Bell et al. (9) reported that a redistribution of assimilates from vegetative dry matter to pods could occur during pod filling under stress caused by high or low temperature and defoliating pathogens.

Components of Resistance

There are no known sources of single gene resistance to Ca in *A. hypogaea* (105). The type of resistance that has been reported in the cultivated peanut is partial. The concept of components of partial resistance, as found in cereals (96), has been applied to peanut. Partial resistance to Ca has been attributed to a number of components (39, 65, 88, 100, 129, 135). Johnson et al. (65) concluded that different components of resistance have additive effects in reducing disease severity.

The evaluation of components of resistance is often complicated by factors such as plant age (90), and pathogen

variability (37). Techniques such as the use of spreader rows, which may generate large amounts of inoculum, may result in masking of partial resistance.

Infection frequency

Infection frequency, defined as the number of lesions per leaf or per unit of leaf area has been used to rank genotypes for resistance to Ca in peanut (88). It has however been shown to be inconsistent in ranking genotypes for resistance to Ca (100), or for Cp (6, 14) in *Arachis hypogaea*.

Inoculum efficiency describes the percentage of successful colonizations per given concentration of propagules applied per unit area. It has been used to rank genotypes for resistance to Ca (134) but has not been found to be a consistent component of resistance to Ca in *A. hypogaea* (100). Waliyar et al. (134) reported that significantly fewer conidia germinated on resistant compared to susceptible genotypes. The resistant genotypes used included interspecific derivatives.

Lesion number per leaf has also been widely used to rank genotypes for resistance to Ca (65, 140) but has not been a consistent component in ranking genotypes for resistance (65). Lesion number however may be an important component in determining disease progress (135).

Culbreath et al. (26) compared peanut genotypes for resistance to Cp by counting the number of stem lesions and the number of lesions per dm of stem length. They reported

3.1 to 9.5 times more lesions per dm of stem length for the susceptible cultivar Florunner compared to the partially resistant cultivar Southern Runner. These differences were also reflected in the pod yields of the two cultivars.

Lesion size

Lesion size has been widely used to rank genotypes for resistance to Ca (100, 134). Waliyar et al. (134) reported significant differences in lesion diameter among genotypes that ranged from 1.2 to 3.0 mm for Ca among some selected genotypes. However, Ricker et al. (100) found no significant differences for lesion diameter among genotypes that varied for different components of resistance to Ca. For Cp, lesion diameter has been shown to be a consistent component in ranking genotypes for resistance both in the field and in the greenhouse (15, 16).

Spore production

Spore production has been shown to be an important component of resistance to Ca and Cp (3, 6, 14, 34, 39, 65, 82, 88, 135, 140). Sporulation, as a component of resistance to Ca, has been classified into three other components which are, duration of spore production or infectious period, spore production per unit of lesion area (34) and maximum percentage sporulating lesions (100). Infectious period has been reported in cereals (96) but has not been reported for Ca or Cp on peanuts. A quantitative method of determining spore production was reported by Foster et al. (34). Subrahmanyam

et al. (128) proposed a 1-5 scale for rating genotypes for amount of spore production.

Maximum percentage sporulating lesions

The maximum percentage of sporulating lesions, is determined by counting the number of lesions per leaf and the number of lesions that are sporulating on a specific date after inoculation. It has been reported to be an important component of resistance to Ca and Cp in peanut. Johnson et al. (65) evaluated 20 Virginia type *A. hypogaea* genotypes for resistance to Ca using latent period, spore production, and percentage of sporulating lesions. Maximum percentage of sporulating lesions was most highly correlated with AUDPC under field conditions. Aquino et al. (6) found maximum percentage sporulating lesions and latent period to be the most highly correlated with Cp development, apparent infection rate and AUDPC.

Incubation period

Incubation period (IP) for is defined as the number of days from inoculation to the appearance of the first visible lesion symptom after inoculation. In greenhouse studies, using the detached leaf technique, Waliyar et al. (134) reported significant genotype differences for Ca ranging from 11.6 days for ICG 6340 to 15.6 days for ICG 8298. In field tests, IP showed no significant differences for Ca (100). For Cp, no significant genotype differences were observed for IP in greenhouse and field tests (14, 140).

Latent period

The latent period (LP) describes the period from inoculation to the production of spores. Latent period has been defined by Shaner (103) as the time from inoculation to the time when 50% of lesions are sporulating, using the probit regression technique (LP50). Johnson et al. (65) used the time from inoculation to the first two sporulating lesions (LP2) to determine latent period. Resistant peanut genotypes have been reported by several authors to have increased latent periods (14, 15, 65, 100, 139). Chiteka et al. (15) showed that latent period measured as the time from inoculation to the first lesion sporulating (LP1) was highly correlated with LP2. Some genotypes with partial resistance to Ca and Cp never attained LP50 (65, 140). Latent period for these genotypes was measured as the time from inoculation to 10% of lesions sporulating (LP10) (140). Aquino et al. (6) found latent period to be one of the components most strongly related to disease progress and to AUDPC for Cp.

Relationships among components

Different components of resistance to Ca have been reported to be related to one another. Foster et al. (34) found that the smallest lesions produced the fewest conidia per lesion and per unit lesion area. Gobina et al. (39) found a correlation between necrotic area and lesions per leaflet on the peanut lines Comet, PI109839, and Tamnut 74.

Ricker et al. (100) evaluated twenty peanut genotypes of *A. hypogaea* using the detached leaf technique. They reported that genotypes with longer latent periods had fewer sporulating lesions and a longer time to leaflet defoliation.

Waliyar et al. (135) determined some components of resistance to Ca in the greenhouse on 19 peanut genotypes that had been reported to be resistant to Ca in the field. Twelve of the genotypes exhibited longer incubation period, reduced sporulation, smaller lesions and lower infection frequencies than susceptible lines. However, some of the lines had a resistant reaction for some components but susceptibility to others. These results concur with observations made by Nevill (88). Significant correlations among components have been reported for Cp (6, 15, 17, 64)

Stability of Resistance

Pathogen variability

The continual use of benomyl to control leaf spot diseases in the southeastern USA resulted in the development of benomyl resistant races of Ca (18, 76). The benomyl-resistant strains identified did not respond to treatment with ten times the recommended rate of benomyl for the control of leaf spot diseases (77).

Subba Rao et al. (126) inoculated four peanut genotypes using eight isolates of Ca from diverse geographic areas. Peanut genotypic variation and Ca isolate differences were

observed for symptom characters, infection frequency and lesion size. These differences were attributed to physiological race differences among the isolates of Ca.

Variations in genotype response to Ca in different locations have been reported (92). The germplasm lines NC3033, PI270806, PI259747, PI350680, PI109839 and GP-NC343 were reported to be resistant to Ca in the USA, but were found to be susceptible in India and in Malawi (92). Wild *Arachis* species *A. chacoense* and *A. stenosperma* were rated as highly resistant to Ca in the USA, but they were found to be susceptible in India and in Malawi (92). Waliyar et al. (136) reported that some peanut genotypes which were rated as resistant to Ca in India showed a variable reaction in West Africa. They attributed this to differences in physiological races prevalent in the different environments. The prevalence of different physiological races of Ca complicates the task of selection and breeding for resistance to Ca. Resistance identified for genotypes in one environment may not necessarily prove to be resistant in a different environment. Resistance to Cp has been shown to be stable in different environments (16, 92, 128, 143).

Effect of temperature

Waliyar et al. (133) studied the effect of temperature on several components of resistance to Ca. The incubation temperature regimes varied from day/night temperatures of 24/24°C to a high of 38/32°C. Lesion numbers were inversely

related to temperature. Levels of the components, lesion number, infection frequency, incubation period, lesion diameter, and necrotic area diameter depended on temperature and genotype. Some genotypes expressed stable resistance levels to Ca across temperatures, and the line 91 PA 150, derived from an interspecific cross, ranked as resistant to all components in all temperature regimes. Other genotypes ranked high on partial resistance to Ca were Ac17894, PI274194, Nc AC 18045 and 91PA 131.

The effect of temperature on sporulation of Ca on peanut leaves incubated at 100% RH was studied by Alderman and Beute (2). Sporulation was found to be greatest at 24 and 28°C intermediate at 20°C and least at 16 or 32°C.

Effect of relative humidity

Sporulation of lesions on peanut leaves infected with Ca was lower as lesion water potential decreased from -0.05 to -6.0MPs (2). They also found that, in cyclic wet and dry periods where the wet period was saturation and the dry period at 78% RH, sporulation increased as the wet period increased.

Inheritance of Resistance

To develop genotypes with resistance to Ca and Cp, a knowledge of the nature and inheritance of resistance is important in the choice of appropriate procedures to employ in the breeding program. Environmental variance, pathogen, and

host variability complicate inheritance studies on peanut leaf spot diseases (143).

Resistance to Ca and Cp has been found to be inherited independently (5, 54). Some negative correlations, however, have been found between resistance to Ca and Cp (49, 85). Anderson et al. (5) attributed this to the possible competition between the two pathogens since all three reports were based on field tests where there was no control of competition. Positive correlations among components of resistance to Ca and Cp were reported (3), indicating possible genetic linkage or host plant physiology that confers resistance to the two diseases.

Sharief et al. (104) studied inheritance of Ca and Cp using crosses involving two tetraploid *A. hypogaea* lines and one diploid wild species *A. cardenasii*. They found that inheritance of Ca and Cp was quantitative and proposed a multifactorial genetic system determining resistance.

Significant maternal effects in the inheritance of resistance to Ca and Cp and reciprocal differences in resistance to Ca and Cp in *Arachis hypogaea*, have been reported, indicating cytoplasmic factors affecting resistance to leaf spot diseases (5, 20, 44). By contrast, Hamid et al. (49) found that there were no maternal or reciprocal effects.

Kornegay et al. (71) studied inheritance of resistance to Ca and Cp using F_1 and F_2 generations of a six parent diallel cross of Virginia type *A. hypogaea*. Resistance to Ca and Cp

was shown to be primarily due to additive genetic effects. Similar results have been reported by Coffelt and Porter (20), Anderson et al. (5), Jogloy et al. (64).

Nevill (89) found no evidence of genetic control of number of lesions per unit leaf area for Cp. He proposed a five locus genetic model to explain inheritance of resistance to Cp.

Heterosis towards the susceptible parents for some components has been reported (5, 89). This suggests some form of dominance for susceptibility in the types of gene action involved. Green and Wynne (44) showed that additive genetic variance alone was not sufficient to account for the observed genetic variation among generation means for several components of resistance to Ca. Observations showed the presence of epistasis for the genotypes involved in the study. Walls and Wynne (138) found that partial resistance to Cp in the F_1 progenies could not be fully explained by a completely recessive model. They suggested the possible involvement of modifier genes at the loci controlling resistance.

Estimates of heritability for components of resistance to Ca have been reported (3, 48, 59). However estimates of narrow sense heritability have been consistently low (Iroume and Knauft, 1987). This suggests that selection for components of resistance to leaf spot diseases in the early generation is not an effective procedure. Anderson et al. (3) concluded that selection among crosses was effective, while

selection within families was of limited value in improving resistance to Ca and Cp in peanuts. However, Chiyembekeza et al. (17) reported moderate to high narrow sense heritability values of 0.62 for latent period, 0.55 for lesion diameter and 0.42 for spore production and realized heritability values of 0.69, 0.63 and 0.51, respectively, for Cp in Malawi. Despite the complex nature of inheritance, progeny with higher yield and greater resistance to leaf spot diseases have been recovered from crosses between adapted lines and low yielding, resistant parents (41).

The objectives of this study were to determine the inheritance of some components of resistance to Ca in peanuts, the relationships among the components, and to evaluate the consistency of the components over seasons and in different environments. Four genotypes that varied in levels of resistance to Ca were crossed in a full diallel, and the progeny were evaluated in Zimbabwe and Florida. The components of resistance that were evaluated were i) latent period (LP), defined as the time from inoculation to the first lesion sporulating, ii) lesion size measured as lesion diameter (LD) mm, iii) amount of spore production determined as a sporulation score using a 1 to 5 scale (SP), (128), and iv) maximum percentage sporulating lesions (MPSL) determined by counting the number of lesions and the number of sporulating lesions.

CHAPTER III

GENETIC VARIABILITY, GENOTYPE X ENVIRONMENT INTERACTIONS AND HERITABILITY FOR SOME COMPONENTS OF RESISTANCE TO EARLY LEAF SPOT IN PEANUT (*ARACHIS HYPOGAEA* L.)

Introduction

Leaf spot diseases caused by *Cercospora arachidicola* Hori. (Ca) and *Cercosporidium personatum* [(Berk. and Curt.) Deighton] (Cp) are among the most important foliar diseases affecting peanuts (70, 94, 105, 116, 143). The two pathogens can be successfully controlled using fungicides (94, 105, 108 117, 118). Fungicides however, are expensive and uneconomical in many developing countries where peanut yields are low, typically (500-800 kg ha^{-1}) (31). In the USA, the use of fungicides to control leaf spot diseases costs an estimated $3.7 million (106). This represents 16% of peanut production costs in the USA annually, and the mounting economic and environmental pressures will demand that high yields be achieved with lower inputs and less fungicide use (105).

The use of disease resistant cultivars is the most economical long term control method. Adapted, high yielding, disease resistant cultivars for a given locality need to be developed. Breeding for resistance to leaf spot diseases is a major objective in peanut breeding programs internationally

(70, 92, 143). There are no known sources of single gene immunity to Ca in *A. hypogaea* (4, 105, 143). A number of sources of partial resistance to Ca have been identified by various scientists (32, 38, 105, 135, 141).

Partial resistance to Ca has been reported in some genotypes in the USA but many of these have been found to be susceptible in Malawi and India (70, 92). Some sources of resistance to Ca identified in India were found to be susceptible in West Africa (141). These findings suggest that some of the sources of resistance to Ca are location specific and that different physiological races of Ca may be prevalent in the different areas. Subba Rao et al. (124) demonstrated the existence of different strains of Ca from different countries.

Partial resistance to Ca has been attributed to a number of components (45, 65, 88, 135). These include incubation period, latent period, amount of spore production, percentage of sporulating lesions, and lesion size. It should be possible to incorporate different components of partial resistance into a desirable cultivar. The effectiveness of this strategy depends on the levels of the components, the environment, and the heritability of the components involved. Many studies on components of resistance to Ca have been conducted in the greenhouse using the detached leaf technique (88, 135). Progeny with higher levels of resistance to Cp

than either parent have been recovered from a cross between a susceptible and a resistant parent for Cp (41).

Inheritance of resistance to Ca and Cp have been reported to be independent (5, 54, 85). However, Anderson et al. (3) reported that inheritance of some physiological mechanisms involved in resistance to the two pathogens may be linked. Many studies on components of resistance have been made in the greenhouse (45, 135). Field evaluations of components of resistance give the best indication of resistance, although they may be subject to larger environmental variance. It would be desirable to determine the consistency of components of resistance measured in different seasons and locations.

The objectives of this study were a) to estimate the levels of some components of resistance to Ca in selected parents and their progeny over different sites and seasons, b) to determine the genetic variability for each of the components, and c) to determine the heritability for these components of resistance to Ca.

Materials and Methods

The parental material used in the tests consisted of four peanut genotypes which varied in their levels of resistance to Ca. The four parents were 97-8-4, 148-7-25, Flamingo, and Southern Runner. Flamingo is a commercial cultivar released in Zimbabwe in 1982 (56). Southern Runner is a commercial cultivar with partial resistance to late leaf spot (40) but it

showed a susceptible reaction to Ca in Zimbabwe (23). Table 3-1 shows the mean seed yields, mean percent defoliation at lifting, and early leaf spot disease scores on the Florida 1-10 scale of the four parent lines compared to the standard commercial cultivars Flamingo and Makulu Red. Makulu Red is a commercial cultivar commonly grown in Zimbabwe and was originally released in Zambia (114). The parent 97-8-4 yielded an average of 30% more than Flamingo in tests conducted at five sites over five seasons in Zimbabwe without the use of fungicides for leaf spot disease control (Table 3-1). In Zimbabwe, Ca is the predominant pathogen (13, 55).

The Diallel Crosses

The four parents were used to make full diallel crosses, including reciprocals, for a total of twelve crosses (Table 3-2). Crosses were made in the greenhouse at Harare Research Station, Zimbabwe during winter, 1990. Further sets of similar crosses were made in Zimbabwe in the greenhouse during winter 1991 and in Gainesville during spring 1995, to produce additional F_1 seed for further evaluation. Summer in Zimbabwe extends from September through April the following year while the winter period runs from May through August.

Site Selection

In order to minimize the effects of mid-season droughts, which are common in December to February in Zimbabwe, a field

Table 3-1. Comparison of five peanut genotypes, Flamingo, Makulu Red, 97-8-4, 148-7-25, and Southern Runner, under unsprayed conditions in Zimbabwe, 1987/88 to 1991/92.

Genotype	Seed[1] yield t ha^{-1}	Yield % of Flamingo	Defo-liation 150 DAP	Disease score[2]
	t ha^{-1}	%	%	Score
Flamingo	2.48	100	68.5	6.2
Makulu Red	2.60	105	70.4	6.5
97-8-4	3.23	130	64.3	4.5
148-7-25	2.50	108	60.2	4.0
S. E. $\pm$	0.28		1.32	0.25
S. Runner[3]	2.30	93	70.2	7.9

[1]Mean seed yield over four sites in five seasons.
[2]Early leaf spot score on the Florida 1-10 scale (14); mean scores over two sites in one season.
[3]Yield from one test in one season.
Source (28)

Table 3-2. Parents and the diallel crosses made to generate F_1 progeny.

Entry No.	Generation	Pedigree
1.	F_1	Flamingo x Southern Runner
2.	F_1	Southern Runner x Flamingo
3.	F_1	Flamingo x 97-8-4
4.	F_1	97-8-4 x Flamingo
5.	F_1	148-7-25 x 97-8-4
6.	F_1	97-8-4 x 148-7-25
7.	F_1	Southern Runner x 148-7-25
8.	F_1	148-7-25 x Southern Runner
9.	F_1	Flamingo x 148-7-25
10.	F_1	148-7-25 x Flamingo
11.	F_1	97-8-4 x Southern Runner
12.	F_1	Southern Runner x 97-8-4
13.	Parent	Flamingo
14.	Parent	Southern Runner
15.	Parent	97-8-4
16.	Parent	148-7-25

with irrigation facilities was selected at Gwebi Variety Testing Center (GVTC) situated 30 km west of Harare. To minimize the effects of natural inoculum, a site that had not been planted to peanut for the previous 10 years was selected 10 km away from the nearest peanut commercial crop. The neighboring fields on all sides of the test were planted to maize to act as a barrier to natural inoculum. In Florida, the tests were conducted at Green Acres Research Farm, 20 km west of Gainesville. The characteristics of the sites selected are shown in Table 3-3.

Progeny Evaluations

The F_1, F_2, and F_3 progeny and the four parents were evaluated for components of resistance over the seasons 1990/91, 1991/92, 1992/93, and 1993/94 in Zimbabwe and in 1995 and 1996 in Florida (Table 3-3). An F_1 population along with the parents, was evaluated in the greenhouse in Gainesville in summer 1995 and in the field in summer 1996. An F_2 population was evaluated in the field at Green Acres Research Farm Gainesville, Florida.

Inoculum production and maintenance

For the tests in Zimbabwe, inoculum of Ca was maintained on the susceptible short season cultivar Natal Common (58), at Harare Research Station.

Table 3-3. Characteristics of the test sites in Zimbabwe and Florida.

	Zimbabwe Gwebi VTC	Florida Green Acres Farm
Latitude	17° 20'S	29° 41'N
Longitude	30° 45'E	82° 30'W
Altitude	1448m	29m
Annual rainfall (Long term average)	800mm	1321mm

Collection and preparation of inoculum

Inoculum was collected from source plants using a cyclone spore collector. Conidial concentrations were determined with a hemacytometer. The suspension of conidia was diluted to 5000 conidia per ml and one drop of Tween 80 surfactant added per 100 ml of suspension to ensure an even spread of conidia on the leaf surface (14).

Sampling and inoculation of test plants

A random sample of disease free representative plants were selected at 45 days after planting (DAP). On each of these, two disease free leaves of approximately the same age were selected at the third and fourth nodes from the growing point of the main stem and tagged for inoculation. These target leaves were inoculated with the suspension of conidia of Ca at 5000 conidia/ml and data on components of resistance were collected from these leaves.

For the Zimbabwe tests, inoculum was applied on target leaves using a Spra Tool (Fisher Scientific Products, Pittsburgh, PA) calibrated to discharge 1 ml of conidial suspension per tetrafoliate leaf. Leaflets of the target leaves were held flat on a small wooden board with the adaxial leaf surface facing upwards and misted for one second with the spore suspension.

Observation of the inoculated leaves was started four days after inoculation and thereafter every two to three days to record the following components of resistance: a) latent

period (LP), b) lesion diameter (LD), c) amount of spore production using a 1-5 scale (128) (SP), and d) maximum percentage sporulating lesions (MPSL).

Components Evaluated

Latent period (LP)

Latent period (LP) was defined as the time in days from inoculation to the first lesion sporulating which was determined by examining the inoculated leaves using a 20x hand lens. A lesion was defined as sporulating when fascicles began to show in the center of the lesion. Target leaves were excised from the plant at 20 to 25 days after inoculation (DAI), and placed in a moist chamber (a petri dish with moist filter paper) for further data collection. Moist chambers were incubated under fluorescent lights at 28°C for 72 hours under a 12 hour light to dark cycle to maximize sporulation, after which LD, SP, and MPSL were then determined.

Lesion diameter (LD)

Three lesions were selected at random for measurement of lesion diameter. Lesions were assumed to be circular and LD was obtained by measuring the diameter of lesions in mm using a transparent ruler.

Sporulation score (SP)

Sporulation score was determined on the same randomly selected lesions by examining them under a 70x dissecting microscope. The amount of spore production was rated using a

1 to 5 scale (SP) according to Subrahmanyam et al. (1982), where: 1=few stromata with little or no sporulation, 2=few stromata with slight sporulation, 3=stromata over most of lesion, moderate sporulation, 4=stromata on entire lesion, moderate to profuse sporulation and 5=dense production of stromata with heavy sporulation.

Maximum percentage sporulating lesions (MPSL)

The total number of lesions on the tetrafoliate leaf (LC) and the number of sporulating lesions (SL) were counted. Percentage sporulating lesions was determined by the relationship MPSL=(SL x 100)/LC.

Tests Conducted

F_1 1990/91 season, Zimbabwe

F_1 seed and the parents were planted on 20 December 1990 at GVTC. Plots were arranged in a randomized complete block design (RCBD) with two replicates and consisted of single rows 3.0 m long spaced at 0.9 m apart and 15 cm between plants within the row. Standard cultural practices for peanut production in Zimbabwe (58) were followed except that no fungicides were applied to control leaf spot diseases. At 45 DAP, a random sample of five plants were selected in each plot. Two fully expanded, disease-free leaves were selected on each plant, were tagged and inoculated with a suspension of conidia of Ca on 10 February, 1991. These leaves were observed every two to three days and data on components of

resistance were collected. Target leaves were excised from the parent plants and placed in a moist chamber on 4 March 1991 and the test was harvested on 25 May, 1991.

F_1 1991/92 season, Zimbabwe

Seed for this test was harvested from crosses made during winter 1991. These were sown on 10 December, 1992 and advanced to the F_2 and were harvested on 31 May, 1992. The planting pattern, design, sampling and inoculation were similar to the 1990/91 test. Plants from cross number 1, (Flamingo x Southern Runner), were confirmed to be selfs and were discarded and excluded from further tests. Plants were sampled and target leaves were inoculated on 3 March, 1992.

F_2 1991/92 season Zimbabwe

The test was planted on 20 December, 1991 in a RCBD with three replicates and plots consisted of three rows x 3.0 m long at 0.9 m apart with seed spaced at 15 cm within the row. A random sample of ten plants per plot were selected on 6 February, 1992, and disease free leaves were tagged, and inoculated as described above. A severe drought was experienced during the 1991/92 season in Zimbabwe. The rainfall received at GVTC for the 1991/92 season is shown in Appendix B.

F_2 1992/93 season, Zimbabwe

The test was planted on 28 December, 1992 using procedures similar to the 1991/92 F_2 test. Target leaves were

inoculated on 20 February, 1993 and excised on 16 March 1993 for incubation and sporulation determination.

F_3 1992/93, Zimbabwe

This test was planted on 28 December, 1992 in plots with 6 rows, 3.0 m long and 0.9 m apart in a RCBD with seed spaced at 15 cm within the row. A total of 18 plants (three plants per row) was selected and target leaves were tagged and inoculated on 20 February, 1993. Target leaves were excised on 16 March, 1996 and prepared as before for further data collection.

F_3 1993/94 season, Zimbabwe

The test was sown on 24 November, 1993 with design, plot size, spacing, sampling, and inoculation procedures similar to the F_3 test of the 1992/93 season. Target leaves were inoculated on 12 January, 1994 and target leaves were excised on 9 February, 1994.

F_1 in greenhouse, Gainesville (1995)

A further set of diallel crosses were made using the parents in the greenhouse in Gainesville during spring 1995. Seed of the parents was planted on 18 February, 1995 and crosses were made in March-April. F_1 seed was harvested on 25 June, dried in the oven at 100°F for five days. Seed of the F_1 population and the parents were planted in the greenhouse in Gainesville on 6 July, 1995. One seed per pot was planted in 30 cm diameter by 20 cm deep polythene pots, filled with metromix 220 (Grace Corp. Lexington Ma.) potting medium.

Seed was treated with ethrel to break dormancy at planting by watering the pots once with a 0.005% solution of ethrel. The design was a RCBD with four replicates and three pots per cross for each replicate. Two additional pots of each of the four parents were planted as a control.

Inoculation Previous attempts to infect susceptible peanut plants with early leaf spot to raise inoculum in the greenhouse in Gainesville, resulted in low infection frequencies, thus making it an inadequate inoculum source. Plants were inoculated by exposing them in a peanut field with a high incidence of early leaf spot, as described for Cp by Watson (140). A peanut field infected with leaf spot diseases in which more than 95 percent of lesions were those of Ca was identified at Mr Shelly Swift's farm in Marion county, situated about 30 miles south of Gainesville. On 21 August, 1995, target leaves were tagged and the 45 day old plants in pots were placed in the peanut field for 72 hours to allow natural infection to take place. The plants were then returned to the greenhouse on 24 August, 1995 for observation and recording of components of resistance. During the exposure period, the weather at the farm was overcast, with trace amounts of rain each day. This provided ideal conditions for infection. Each pot was watered with 1.5 liters of water each day to ensure adequate moisture and encourage successful infection. Daily maximum, minimum temperature in the greenhouse were recorded from 16 July to

23rd September 1995 in order to cover the duration from inoculation to the end of data collection (Appendix C). Two pots of each parent were left in the greenhouse to act as an uninoculated control.

Peanut leaves infected with Ca were collected from the field for use as an inoculum source for further tests in the field the following season.

F, field test, Gainesville 1996

Plots consisted of non replicated single rows 6.15 m long with plants spaced at 0.30 m within the row, were planted on 6 May, 1996. Standard cultural practices were used for the test (142), except that no fungicides were applied to control diseases. Six plants were randomly selected from each plot and two disease free leaves per plant were tagged and inoculated on 22 June, 1996.

Inoculation procedure Peanut leaves infected with Ca collected from peanut plants from the farm in Marion County in 1995 were shredded and used as a source of inoculum. Plants to be inoculated were first drenched with water to ensure the target leaves were thoroughly wetted. Inoculation was accomplished by gently rubbing 0.5 g of moist leaf debris on the target leaf. Inoculations were made in the evening at 8:00 pm ET when the temperatures were low enough to allow prolonged leaf wetness to encourage germination of conidia. For three days after inoculation, the target plants were watered every evening to ensure maximum leaf wetness to

encourage infection. Data on components of resistance were collected as previously described until the target leaves were excised from the parent plants on 16 July, 1996. Data on components of resistance were collected using procedures described before.

F_2 field test, Gainesville (1996)

This test was planted at Green Acres Research Farm approximately 20 km west of Gainesville. Seed for this test was harvested from the F_1 greenhouse test of 1995 and was planted on 6 May, 1996. Experimental design was a RCBD with two replicates and plots consisted of four rows 6.15 m long 0.92 m apart, with seed sown 0.30 m spacing within the row. Agronomic practices were followed as for the F_1 field test in Gainesville, 1996. A random sample of six representative plants per plot was selected on 19 June, 1996 and two target leaves were tagged on each plant. The first replicate was inoculated with Ca on 20 June, 1996 and the second replicate was inoculated on 21 June, 1996. Inoculation was achieved using the same process described for the F_1 field plots in Gainesville.

Data collection Data on components of resistance were collected on the target leaves in the field until they were excised from the parent plants on 15 July 1996 and then placed in moist chambers for completion of data collection.

Statistical Analysis

Analysis of variance was performed on plot means for each component. Due to the drought experienced during the 1991/92 season, variable numbers of seed were harvested from plants with some plots yielding no seed. This resulted in unequal numbers of plants per plot for different crosses. The least squares means were computed using the univariate procedure of the SAS program (78). The type III sum of squares was used to generate mean squares. Percentage sporulating lesions was transformed using the square root transformation to give a transformed value $(TMPSL)=(MPSL + 0.5)^{1/2}$. Analysis was carried out using the model $Y_{ijk} = \mu + G_i + \beta_j + \epsilon_{ijk}$, where Y_{ijk} = the k th mean of observations in block j for the i th entry; G_i = effect of entry (i=1 to 16); β_j = effect of block (replication) (j=1 to 4); and ϵ_{ijk} = random error.

For the populations that were evaluated in two or more different seasons, further analyses of variance was carried out using the model $Y_{ijkl} = \mu + G_i + \beta_j + \alpha_l + G\alpha_{il} + \epsilon_{ijkl}$, where Y_{ijkl} is the l th mean of observations of the k th year in block j for the i th entry, μ=overall mean; G_i is the effect of entry (i=1 to 16); β_j is the effect of block (j=1 to 2); α_l is the effect of year (l=1 to 2); and $G\alpha_{il}$ is the entry x year interaction; and ϵ_{ijkl} represents the random error.

To estimate narrow sense heritabilities for the four components, the parent-offspring regression analysis (120) on the pooled data was used. The estimator equation is given as

$h^2 = b/2r_{xy}$ where r_{xy} is a measure of the degree of genetic relationship between the parent y and its offspring x, and b is the slope of the regression of parent on offspring. The value of b in the case of a self pollinated crop such as peanut, is equivalent to the narrow sense heritability.

Results and Discussion

Lesions developed on 95 to 100% of leaves inoculated using all three methods except for the F_1 test conducted in the 1991/92 season. This is the first time the inoculation procedure using an exposure method described by Watson (140) has been reported with early leaf spot on peanuts. Lesion numbers were low in the F_1 test conducted in 1991/92 and lesions did not develop on some of the inoculated plants in this test. Due to drought conditions in Zimbabwe, early leaf spot disease developed on less than 50% of target leaves in this test and the number of samples with successful lesion development was small and precluded analysis of data. In the greenhouse test in Gainesville, 1995, no lesions developed on the control plants. This indicated that the inoculation procedure by exposure to the field was effective.

Tests for normality using the box plot procedure of SAS (78) showed the data for LP, LD, and SP to be normally distributed, except for percentage data for maximum percentage of sporulating lesions (MPSL). Analysis of variance for percentage sporulating lesions was conducted on square root

transformed data but results for this component are reported on the untransformed data. Results of analysis of variance on components of resistance in each test are summarized in Table 3-4. Means for the crosses and parents for the four components of resistance are shown in Tables 3-7 to 3-19. Plants of cross 1 (Flamingo x Southern Runner) were confirmed to be selfs in the F_1 generation, and F_1 plants of cross number 4 (97-8-4 x Flamingo), did not produce viable F_2 seed due to the drought in 1991/92. These two crosses were excluded from analysis hence there were no results for reciprocals presented for the crosses involved.

Latent Period (LP)

There were significant differences ($P \leq 0.05$) among entries for LP in all seasons except for the F_1 test in Zimbabwe in 1990/91 (Table 3-4). This indicates that genetic variability for LP among entries exists. The overall mean LP for the different tests ranged from 15.0 days for the F_2 test in Florida in 1996 to a high of 24.4 days in the F_2 test in Zimbabwe in 1991/92 (Table 3-8). For the majority of tests, the mean LP for all entries ranged from 15 to 20 days (Tables 3-7 to 3-9). The mean LP for the F_2 test in 1991/92 (Table 3-8) was relatively high when compared to other tests. This is attributed to the severe drought experienced during that season. The longer latent period was caused by delayed sporulation caused by moisture stress. Total monthly rainfall

Table 3-4. Significance of F values for components of resistance to early leaf spot in all tests.

Generation and season	Component[1] LP	LD	SP	TMPSL
Zimbabwe				
F_1 1990/91	ns[2]	*	ns	ND[4]
F_2 1991/92	*	ns	ns	*
F_2 1992/93	***	***	ns	ns
F_3 1992/93	***	**	ns	***
F_3 1993/94	***	*	**	*
Florida				
F_1 1995 gh[3]	***	*	***	*
F_1 1996	***	ns	***	***
F_2 1996	**	ns	***	***

[1]LP=latent period (days), LD=lesion diameter in mm, SP=sporulation score on a 1-5 scale, TMPSL=square root transformed maximum percentage sporulating lesions.
[2]Significance is denoted by *, **, and ***, at the $P \leq 0.05$, 0.01, and 0.001 levels, respectively.
[3]1995 Florida test was conducted in a greenhouse using plants exposed to natural inoculum.
[4]No data.

for the 1991/92 season at GVTC is shown in Appendix B. The extended period of drought resulted in reduced leaf water potential and plants were observed to be wilted for some periods during the day, concurrent with the period when disease developed and evaluation for components of resistance was in progress. Alderman and Beute (2) found that sporulation of Ca was greater when leaf moisture was near saturation but declined with decreasing water potential from -4Mpa. They found no conidia on peanut leaves infected with Ca at -6Mpa.

The range in mean LP for entries varied from a low of 3 days to a high of 12 days (Table 3-8). The lowest ranges were for the F_2 in the 1992/93 (Table 3-8) and in the F_3 test in 1993/94 (Table 3-9). The period following inoculation in both these tests coincided with periods of continuous rainfall and high humidity. These conditions encouraged more spore production thereby reducing the latent period.

Southern Runner had the shortest LP in all tests except for the F_2 test in 1991/92 (Table 3-8). However, the LP for this cultivar was not significantly different from the cross, Southern Runner x 148-7-25, which had the shortest LP in this test. This indicates the consistency of LP in ranking genotypes for resistance to Ca. Latent period has been shown to be a consistent component for rating peanut genotypes for resistance to Ca (65, 88, 100). The genotypes 97-8-4 and 148-7-25 ranked the highest for LP in five of the tests and ranked

among the best three in two of the remaining tests (Tables 3-7 to 3-9). The parent 97-8-4 ranked second or better in six of the tests. This further supports consistency of LP in rating genotypes for resistance to Ca.

There was a significant year effect ($P \leq 0.05$) and a significant cross x year interaction ($P \leq 0.05$) for LP (Table 3-5 and 3-6). This indicates that the length of the LP is dependent on environment. The evaluation of resistance to Ca should be conducted over multiple sites and seasons in order to improve reliability. All resistance that has been reported in the cultivated peanut is partial and has been attributed to the different components of resistance (88, 135). This variation in LP may contribute in explaining the observed fact that genotypes resistant to early leaf spot in one location may be susceptible in other locations as noted by Nigam et al. (92), and Waliyar et al. (135). There have been few reports of determinations of LP in the field in multiple seasons and over different locations. These results show the extent of environmental variability for LP that can be expected in breeding for resistance to Ca under field conditions and the level of resistance to Ca as measured by latent period among the parents and their progeny. The performance of the four parent lines with respect to latent period in diverse environments has been quantified.

Table 3-5. Combined analysis of variance for components of resistance to early leaf spot for the F_2 generation over two seasons in Zimbabwe[1].

Source	df	Component[2] mean square			
		LP	LD	SP	TMPSL
Reps	2	14.12ns[3]	0.05ns	0.04ns	0.98ns
Entries	13	19.96**	0.24ns	0.21ns	1.84ns
Year	1	1690.23***	10.50**	4.56***	42.72***
Year x Entry	13	15.63**	0.24ns	0.12ns	1.70*

[1]Data for the 1991/92 and 1992/93 seasons were combined for analysis.
[2]LP=latent period (days), LD=lesion diameter in mm, SP=sporulation score on a 1-5 scale, TMPSL=square root transformed maximum percentage sporulating lesions.
[3]Significance is denoted by *, **, and ***, at the $P \leq 0.05$, 0.01, and 0.001 levels, respectively.

Table 3-6. Combined analysis of variance for components of resistance to early leaf spot for the F_3 in Zimbabwe[1].

Source	df	Component[2] mean square			
		LP	LD	SP	TMPSL
Reps	3	17.43***[3]	0.12ns	0.59***	4.82**
Entries	3	8.48**	0.29ns	0.20ns	2.49ns
Year	1	192.50***	0.48**	8.46**	0.22*
Year x Entry	13	3.35***	0.13ns	0.10ns	1.00ns

[1]Data for the 1992/93 and 1993/94 seasons were combined for analysis.
[2]LP=latent period (days), LD=lesion diameter in mm, SP=sporulation score on a 1-5 scale, TMPSL=square root transformed maximum percentage sporulating lesions.
[3]Significance is denoted by *, **, and *** at the $P \leq 0.05$, 0.01, and 0.001 levels, respectively.

Table 3-7. Means for latent period (days) for the F_1 generation in Florida and Zimbabwe.

Pedigree	Florida 1995 gh[1]	Florida 1996	Zimbabwe 1990/91
148-7-25	20.2a[2]	16.8ad	22.8
148-7-25 x 97-8-4	19.0ab	16.2bc	21.2
97-8-4	18.9ab	17.9a	25.5
148-7-25 x Flamingo	18.8a-c	17.1a-c	23.6
97-8-4 x 148-7-25	18.7a-d	16.9a-c	17.3
Flamingo x 148-7-25	18.3a-e	16.4b-d	20.7
Flamingo	18.3a-e	17.3ab	22.1
Flamingo x 97-8-4	17.5b-e	16.2c	19.8
148-7-25 x S. Runner	17.1b-f	14.6e	22.8
Flamingo x S. Runner	17.0b-f	14.3ef	21.9
S. Runner x Flamingo	16.9b-f	13.2f-h	17.3
S. Runner x 97-8-4	16.4c-f	12.9hg	16.0
S. Runner x 148-7-25	16.3d-g	13.7e-g	15.5
97-8-4 x Flamingo	16.3e-g	16.7cd	21.3
97-8-4 x S. Runner	14.7fg	15.7d	18.8
S. Runner	14.2fg	12.5h	15.5
Mean	17.4	15.5	21.0
P>F[3]	***	***	ns
Range	6.0	4.8	8.1

[1]The 1995 Florida test was conducted in a greenhouse.
[2]Means followed by the same letter are not significantly different (P>0.05).
[3]Significance is denoted by *, **, and ***, at the $P \leq 0.05$, 0.01, and 0.001 levels, respectively.

Table 3-8. Means for latent period (days) for the F_2 generation in Zimbabwe and Florida.

Pedigree	Zimbabwe 1991/92	Zimbabwe 1992/93	Florida, 1996
97-8-4	29.3a[1]	14.3de	18.1a
97-8-4 x Flamingo	27.0ab	15.0b-e	15.5be
148-7-25 x S. Runner	27.0ab	14.8c-e	15.9ad
Flamingo x 148-7-25	26.5ab	17.0a	14.8b-f
148-7-25 x 97-8-4	26.2a-c	16.2ab	15.4b-e
148-7-25 x Flamingo	25.4a-c	15.9a-c	16.4a-c
Flamingo	25.3a-c	15.3b-e	15.2c-e
97-8-4 x S. Runner	25.1a-c	15.3b-e	14.4c-f
148-7-25	24.1a-d	16.7ab	17.3ab
Flamingo x S. Runner	24.1a-d	-	12.8ef
97-8-4 x Flamingo	24.1a-d	-	14.7b-f
S. Runner x Flamingo	23.8a-d	14.7c-e	14.0c-f
97-8-4 x 148-7-25	23.6a-d	14.5ed	15.7a-d
S. Runner	20.0b-d	14.0e	12.4f
S. Runner x 97-8-4	19.0cd	16.0ab	13.8c-f
S. Runner x 148-7-25	17.2d	14.0e	13.6e-f
Mean	24.4	15.2	15.0
P>F[2]	*	***	**
Range	12.1	3.0	5.7

[1]Means followed by the same letter are not significantly different (P>0.05).
[2]Significance is denoted by *, **, and ***, at the P≤0.05, 0.01, and 0.001 levels, respectively.

Table 3-9. Means for latent period (days) for the F_3 generation in two seasons 1992/93 and 1993/94 in Zimbabwe.

Pedigree	Zimbabwe 1992/93	Zimbabwe 1993/94
97-8-4 x S. Runner	19.2a[1]	21.0abc
97-8-4 x 148-7-25	18.7ab	21.6a
97-8-4 x Flamingo	18.5a-c	-
148-7-25 x 97-8-4	18.3a-c	19.3cd
Flamingo	18.2a-d	20.9abc
148-7-25	18.0a-d	19.7bcd
Flamingo x 97-8-4	18.0a-d	19.8abc
148-7-25 x S. Runner	17.9a-d	19.7bcd
148-7-25 x Flamingo	17.7a-d	20.5bcd
97-8-4	17.4b-e	20.8abc
Flamingo x 148-7-25	17.0c-e	19.6bcd
Flamingo x S. Runner	16.7de	-
S. Runner x Flamingo	16.6de	21.2abc
S. Runner x 148-7-25	16.2ef	18.1de
S. Runner x 97-8-4	15.2fg	21.0abc
S. Runner	14.0g	18.1de
Mean	17.4	20.1
$P>F$[2]	***	***
Range	5.2	3.5

[1]Means followed by the same letter are not significantly different (P>0.05).
[2]Significance is denoted by *, **, and ***, at the $P\leq 0.05$, 0.01, and 0.001 levels, respectively.

Lesion Diameter (LD)

There were significant differences ($P \leq 0.05$) among crosses for LD for the tests in Zimbabwe, except for the 1991/92 F_2 test (Table 3-4). In the tests in Florida, significant differences for LD were noted only in the F_1 greenhouse test in 1995 (Table 3-4).

Mean LD for different tests ranged from 2.18 (Table 3-11) to 3.41 mm (Table 3-10). In the F_1 test in Zimbabwe, LD ranged from 2.34 to 3.10 mm. An examination of the ranks of entries (Table 3-10 to 3-12) shows that LD is not a consistent component for rating genotypes for resistance to early leaf spot in different environments. The genotype 97-8-4 ranked number 15 in the F_1 test in Zimbabwe but the same parent had the smallest lesions in the F_1 greenhouse test in Gainesville (Table 3-10).

Lesions on the plants in these tests were noted to be very irregular with rather diffuse margins, sometimes with a yellow halo of varying size. These symptoms are typical of Ca on peanuts as described by Subba Rao et al. (126). However, this factor may have been confounded with the actual necrotic leaf area during measurement. Although significant differences ($P \leq 0.05$) were noted for some tests, no significant differences for LD were noted in three of the tests. These results agree with those by Ricker et al. (100) who found no significant differences among 20 peanut genotypes with partial resistance to Ca as measured by LD in the greenhouse in North

Table 3-10. Means for lesion diameter (mm) for the F_1 generation in Zimbabwe and Florida.

Pedigree	Zimbabwe 1990/91	Florida 1995[1]	Florida 1996
S. Runner	2.34d[2]	3.36bcd	3.21
Flamingo x 97-8-4	2.38d	3.94ab	3.25
148-7-25 x Flamingo	2.39d	4.07bcd	3.22
148-7-25 x 97-8-4	2.40d	3.00cd	3.25
S. Runner x 97-8-4	2.45cd	3.01cd	2.89
97-8-4 x S. Runner	2.53bcd	3.70abc	3.35
148-7-25 x S. Runner	2.58bcd	3.48a-d	3.67
Flamingo x S. Runner	2.59bcd	3.48abc	3.40
148-7-25	2.63bcd	3.44a	3.53
97-8-4 x 148-7-25	2.63bcd	3.19abc	3.04
Flamingo	2.67a-d	3.48a-d	3.70
S. Runner x 148-7-25	2.76a-d	3.45a-d	3.30
Flamingo x 148-7-25	2.80a-d	3.42a-d	3.42
97-8-4 x Flamingo	2.90abc	3.23bcd	3.05
97-8-4	2.98ab	3.74d	3.00
S. Runner x Flamingo	3.10a	3.57abc	3.32
Mean	2.63	3.41	3.28
P>.F[3]	*	*	ns
Range	0.77	1.32	0.81

[1]The 1995 Florida test was conducted in a greenhouse.
[2]Means followed by the same letter are not significantly different (>0.05).
[3]Significance is denoted by *, **, and ***, at the $P \leq 0.05$, 0.01, and 0.001 levels, respectively.

Table 3-11. Means for lesion diameter (mm) for the F_2 generation in Zimbabwe and Florida.

Pedigree	Zimbabwe 1991/92	Zimbabwe 1992/93	Florida 1996
97-8-4 x S. Runner	1.96	3.05ab[1]	3.43
Flamingo x 97-8-4	1.97	3.12ab	3.90
S. Runner x 97-8-4	2.03	2.86abc	3.38
97-8-4 x Flamingo	2.04	-	3.34
148-7-25	2.06	3.05ab	3.43
Flamingo x S. Runner	2.07	-	3.04
S.Runner	2.07	2.45cd	3.31
148-7-25 x Flamingo	2.08	2.98abc	3.51
S. Runner x Flamingo	2.09	3.17ab	3.42
97-8-4	2.10	3.39a	3.08
97-8-4 x 148-7-25	2.13	2.60bcd	3.17
S. Runner x 148-7-25	2.24	2.12d	3.03
148-7-25 x 97-8-4	2.28	2.97abc	2.96
148-7-25 x S. Runner	2.32	3.20a	3.31
Flamingo x 148-7-25	2.58	2.96abc	3.23
Flamingo	2.83	3.05ab	3.54
Mean	2.18	2.93	3.32
P>F[2]	ns	**	ns
Range	0.87	1.27	0.94

[1]Means followed by the same letter are not significantly different (P>0.05).
[2]Significance is denoted by *, **, and ***, at the P≤0.05, 0.01, and 0.001 levels, respectively.

Table 3-12. Means for lesion diameter (mm) for the F_3 generation in two seasons in Zimbabwe.

Pedigree	1992/93	1993/94
Flamingo x 97-8-4	2.83	2.88d[1]
S. Runner x Flamingo	3.00	3.05cd
Flamingo	3.02	3.18bcd
97-8-4 x Flamingo	3.05	3.20bcd
S. Runner	3.09	3.04cd
97-8-4 x S. Runner	3.14	3.72ab
148-7-25 x S. Runner	3.15	3.42abc
Flamingo x S. Runner	3.16	3.08cd
97-8-4 x 148-7-25	3.21	3.19bcd
S. Runner x 97-8-4	3.20	3.73ab
Flamingo x S. Runner	3.23	-
97-8-4 x Flamingo	3.26	-
148-7-25 x Flamingo	3.28	3.31a-d
148-7-25	3.30	3.76a
148-7-25 x S. Runner	3.35	3.49abc
Flamingo	3.55	3.12cd
Mean	3.18	3.26
P>F[2]	ns	**
Range	0.72	0.88

[1]Means followed by the same letter are not significantly different (P>0.05).
[2]Significance is denoted by *, **, and ***, at the $P \leq 0.05$, 0.01, and 0.001 levels, respectively.

Carolina. In contrast, Waliyar et al. (135) reported lesion diameter to be consistent in ranking genotypes for resistance to early leaf spot using Indian sources of resistance to early leaf spot. Waliyar et al. (134) reported LD to be temperature dependent.

Although LD was not consistent in rating genotypes for Ca resistance, it is an important epidemiological component of resistance since it is related to the total leaf necrotic area.

There were significant year effects ($P \leq 0.05$) but the entry x year interaction was not significant $P \leq 0.05$) on LD (Table 3-5 and 3-6). Reports of consistent rankings of genotypes for LD have been from greenhouse tests and from field tests where components of resistance have been evaluated under controlled conditions using the detached leaf technique (88, 135). This consistency may not be reflected under field conditions. Lesion diameter alone may not be a reliable parameter to use in assessing genotypes for resistance to early leaf spot.

Sporulation Score (SP)

There were significant differences among crosses ($P \leq 0.05$) in the F_3 test of 1993/94 in Zimbabwe (Table 3-4). In Florida, significant differences for SP ($P \leq 0.01$) were noted for all tests (Table 3-4). Significant differences among entries were noted in only 4 out of 8 tests. This indicates that although genetic variability exists for this components,

it is more sensitive to environmental variance compared to some other components. Significant differences for sporulation score have been reported by other authors for SP (65, 88, 133, 135). In these tests, the amount of spore production was reported to be a strong and consistent component of rate reducing resistance. Spore production is important for early leaf spot epidemic development in the field since it is responsible for the production of new propagules that give rise to new infections.

The mean values of SP for tests ranged from 1.30 to 2.36 in the F_1 greenhouse test in 1995. Across tests, the range for SP was 0.36 for the F_3 test in 1992/93 (Table 3-15) to 1.78 for the F_2 test in Florida, 1996 (Table 3-14). Genetic variability exists among the entries for amount of spore production. Expression of these differences however depended on the environment. Spore production of Ca is dependent on leaf moisture status (2). Higher moisture levels result in abundant sporulation while lower moisture results in reduced spore production.

The parent 148-7-25 had the least spore production per lesion in two of the tests (Table 3-13) and was as good as the best entry in all the other tests. Southern Runner produced the most spores per lesion in three of the tests and was similar to the highest in spore production in seven of the tests conducted. Spore production for Flamingo and 97-8-4 was similar to that for 148-7-25. These results show that

Table 3-13. Means for sporulation score for the F_1 generation in Zimbabwe and Florida[1].

Pedigree	Zimbabwe 1990/91	Florida 1995 gh[2]	Florida 1996
148-7-25	1.00	1.30d[3]	1.08f
148-7-25 x S. Runner	1.10	1.70cd	1.97abc
148-7-25 x Flamingo	1.12	1.42dd	1.25f
148-7-25 x 97-8-4	1.22	1.72cd	1.39cde
Flamingo x 148-7-25	1.24	1.40d	1.29ef
Flamingo	1.30	1.70cd	1.19f
97-8-4 x S. Runner	1.33	2.00abc	2.28a
97-8-4 x Flamingo	1.37	1.76bcd	1.30f
Flamingo x S.Runner	1.38	2.10abc	2.17ab
97-8-4 x 148-7-25	1.39	1.83a-d	1.47def
S. Runner	1.49	2.05abc	1.63cde
S. Runner x Flamingo	1.53	2.31ab	2.25a
97-8-4	1.58	1.60cd	1.17f
Flamingo x 97-8-4	1.65	1.76bcd	1.19f
97-8-4 x S. Runner	1.66	2.36a	1.83bc
S. Runner x 148-7-25	2.35	1.78abc	1.71cd
Mean	1.50	1.80	1.57
P>F[4]	ns	**	***
Range	1.35	1.06	1.10

[1]Sporulation score was determined using a 1 to 5 scale in which 1=few stromata with little sporulation and 5=dense production of stromata with heavy sporulation.
[2]The 1995 Florida test was conducted in a greenhouse.
[3]Means followed by the same letter are not significantly different (P>0.05).
[4]Significance is denoted by *, **, and ***, at the $P \leq 0.05$, 0.01, and 0.001 levels, respectively.

Table 3-14. Means for sporulation score for the F_2 generation in Zimbabwe and Florida[1].

Pedigree	Zimbabwe 1991/92	Zimbabwe 1992/93	Florida 1996
Flamingo	1.09	2.04	1.44e-h[2]
148-7-25 x Flamingo	1.50	2.00	1.36fgh
Flamingo x S. Runner	1.35	-	2.21c-d
97-8-4 x Flamingo	1.40	-	1.50e-h
148-7-25 x 97-8-4	1.42	1.84	1.05h
148-7-25	1.42	2.03	1.18hg
S. Runner x 97-8-4	1.43	2.03	1.86c-f
97-8-4	1.51	1.97	1.63efg
S. Runner x 148-7-25	1.54	2.5	1.94c-e
97-8-4 x 148-7-25	1.61	1.92	1.40e-h
148-7-25 x S. Runner	1.62	1.85	1.70d-f
Flamingo x 148-7-25	1.67	2.33	1.31fgh
S. Runner x Flamingo	1.69	2.06	2.46efg
Flamingo x 97-8-4	1.82	2.15	1.31fgh
97-8-4 x S. Runner	2.01	2.06	2.36abc
S. Runner	2.06	2.27	2.83a
Mean	1.54	2.07	1.72
P>F[3]	ns	ns	***
Range	0.95	0.43	1.78

[1]Sporulation score was determined using a 1 to 5 scale in which 1=few stromata with little sporulation and 5=dense production of stromata with heavy sporulation.
[2]Means followed by the same letter are not significantly different (P>0.05).
[3]Significance is denoted by *, **, and ***, at the $P \leq 0.05$, 0.01, and 0.001 levels, respectively. (P>0.05).

Table 3-15. Means for sporulation score for the F_3 generation in two seasons in Zimbabwe[1].

Pedigree	Season 1992/93	Season 1993/94
148-7-25 x Flamingo	1.86	1.36bc[2]
97-8-4 x S. Runner	1.96	1.44bc
148-7-25	1.97	1.28c
97-8-4 x Flamingo	1.97	-
Flamingo x 148-7-25	2.00	1.25c
148-7-25 x 97-8-4	2.00	1.46bc
148-7-25 x S. Runner	2.01	1.41bc
Flamingo x 97-8-4	2.02	1.19c
Flamingo	2.02	1.44c
97-8-4 x 148-7-25	2.02	1.21c
S. Runner x 97-8-4	2.02	1.43c
Flamingo x S. Runner	2.02	-
S. Runner x Flamingo	2.05	1.39c
97-8-4	2.06	1.40bc
S. Runner	2.13	2.18a
S. Runner x 148-7-25	2.18	1.89ab
Mean	2.02	1.46
P>F[3]	ns	**
Range	0.36	0.99

[1]Sporulation score was determined using a 1 to 5 scale in which 1=few stromata with little sporulation and 5=dense production of stromata with heavy sporulation.
[2]Means followed by the same letter are not significantly different (P>0.05).
[3]Significance is denoted by *, **, and ***, at the $P \leq 0.05$, 0.01, and 0.001 levels, respectively.

sporulation score was a consistent component in rating the entries for resistance to early leaf spot. Entries that had low sporulation in this test also had low sporulation at different sites and in different seasons.

There were significant year effects ($P \leq 0.05$) although the entry x year interaction was not significant ($P > 0.05$), (Tables 3-5 and 3-6). This reinforces the consistency of SP in rating genotypes for resistance to early leaf spot. Although no significant differences were noted in the 1990/91 F_1 and the 1991/92 F_2 tests in Zimbabwe, the ranking of the entries generally were closely comparable with other tests. Four entries ranked among the best six in all three F_1 tests while four entries were among the lowest ranking six entries in all three F_1 tests from different environments. This indicates consistency of SP in ranking entries for resistance to early leaf spot. Differences among genotypes for SP were highly significant ($P \leq 0.001$) in Florida but in Zimbabwe, significant differences ($P \leq 0.05$) were noted in only one of five tests (Table 3-4). It appears that differences among entries were more markedly expressed in Florida than in Zimbabwe. Environmental conditions appear to strongly influence the expression of this component among genotypes.

Maximum Percentage Sporulating Lesions (MPSL)

There were significant differences among crosses ($P \leq 0.05$) for MPSL in all tests but the 1992/93 F_2 test in Zimbabwe

(Table 3-4). The overall mean MPSL values from different tests ranged from 28.3% for the 1992/93 F_2 field test in Zimbabwe (Table 3-18), to 49.7% in the 1996, F_2 field test in Florida (Table 3-16). In the F_2 test in Florida, MPSL ranged from 14.7 to 64.3% (Table 3-16). In the Zimbabwe F_3 tests, entry means for MPSL ranged from 24.1 to 52.4% in 1992/93 test and 29.5 to 52.0 in the 1993/94 tests (Table 3-18) which were similar. The parent, 148-7-25 had MPSL values which were among the best three entries in all tests (Tables 3-16 and 3-17). The ranking of 97-8-4 for MPSL was not consistent in different tests. It ranked number 15 in the 1991/92 F_2 test in Zimbabwe but ranked number 1 in the greenhouse test in 1995 in Florida. It appears that this component was irregular in the case of this parent. Flamingo ranked similarly in all tests. Southern Runner ranked among the five entries with the highest MPSL and did not differ significantly from the worst entry in all cases. These results indicate that there is genetic variability for MPSL among these crosses. Selection of genotypes with reduced MPSL should be possible. The results agree with those reported by Ricker et al. (100) and Johnson et al. (65). Johnson et al. (65) found MPSL to be the component to be the most highly correlated with AUDPC and with disease progress in the field. They also reported significant $P \leq 0.01$) differences in MPSL among selections derived from the same cross indicating that selection for reduced MPSL within a cross would be effective.

Table 3-16. Means for maximum percentage sporulating lesions for the F_1 generation in Gainesville, Florida.

Pedigree	Florida 1995 gh[1]	Florida 1996
97-8-4	20.6d[2]	23.5de
148-7-25 x Flamingo	21.3d	31.8cd
Flamingo x 148-7-25	24.5d	24.5de
148-7-25	25.4bcd	14.7e
148-7-25 x 97-8-4	26.0bcd	29.4cde
Flamingo	29.9bcd	27.9cde
148-7-25 x S. Runner	30.7a-d	52.3ab
S. Runner x 97-8-4	31.1a-d	55.9ab
97-8-4 x 148-7-25	33.2a-d	31.5cd
97-8-4 x Flamingo	33.2a-d	26.8cde
Flamingo x 97-8-4	34.8a-d	29.8cd
Flamingo x S. Runner	38.8a-d	55.4ab
S. Runner x 148-7-25	40.6a-d	40.6bcd
97-8-4 x S. Runner	46.1abc	43.3abc
S. Runner	47.6ab	22.5de
S. Runner x Flamingo	53.4a	64.3a
Mean	39.9	34.7
P>F[3]	***	*
Range	32.6	49.7

[1]The 1995 Florida test was conducted in a greenhouse.
[2]Means followed by the same letter are not significantly different (P>0.05).
[3]Significance is denoted by *, **, and *** at the $P \leq 0.05$, 0.01, and 0.001 levels, respectively.

Table 3-17. Means for maximum percentage sporulating lesions for the F_2 generation in Zimbabwe and Florida.

Pedigree	Zimbabwe 1991/92	Zimbabwe 1992/93	Florida 1996
Flamingo	16.2c	26.0	28.9fe[1]
148-7-25 x 97-8-4	20.0bc	21.9	25.5f
148-7-25 x Flamingo	32.6abc	24.7	24.6f
148-7-25	32.7abc	21.9	27.4f
Flamingo x S. Runner	34.3abc	-	46.6bcd
97-8-4 x S. Runner	34.7abc	25.7	68.1a
S. Runner x 97-8-45	35.6abc	21.0	53.1bcd
S. Runner x Flamingo	42.3ab	20.5	63.4ab
148-7-25 x S. Runner	44.1a	19.1	44.9b-e
Flamingo x 148-7-25	48.6a	24.0	29.0c-f
S. Runner x 148-7-25	48.6a	24.0	46.2bcd
97-8-4 x Flamingo	49.3a	-	35.8c-f
Flamingo x 97-8-4	49.4a	23.0	30.9def
S. Runner	50.4a	33.0	60.5ab
97-8-4 x 148-7-25	55.2a	20.2	27.4ef
97-8-4	58.9a	21.5	29.5f
Mean	40.6	23.8	38.9
P>F[2]	*	ns	**
Range	33.7	13.8	22.6

[1]Means followed by the same letter are not significantly different (P>0.050).
[2]Significance is denoted by *, **, and ***, at the $P \leq 0.05$, 0.01, and 0.001 levels, respectively.

Table 3-18. Means for maximum percentage sporulating lesions for the F_3 generation for two seasons in Zimbabwe.

Pedigree	Season 1992/93	Season 1993/94
148-7-25 x Flamingo	24.1e[1]	33.8a-d
148-7-25	26.7e	29.7cd
148-7-25 x 97-8-4	28.3de	33.5a-d
148-7-25 x S. Runner	30.7cde	34.1abc
Flamingo x S. Runner	31.6cde	-
Flamingo	32.5b-e	36.0abc
Flamingo x 97-8-4	40.3a-d	32.1abc
Flamingo x 148-7-25	40.7a-d	38.6abc
97-8-4 x Flamingo	41.7a-d	-
S. Runner x 148-7-25	43.8bc	52.0a
S. Runner x 97-8-4	44.1abc	40.7abc
S. Runner	45.2abc	50.0ab
S. Runner x Flamingo	45.4abc	42.4abc
97-8-4 x S. Runner	47.2ab	37.8abc
97-8-4	51.4a	42.2abc
97-8-4 x 148-7-25	52.4a	29.5cd
Mean	38.6	37.5
P>F[2]	***	*
Range	28.3	22.5

[1]Means followed by the same letter are not significantly different (P>0.05).
[2]Significance is denoted by *, **, and ***, at the $P \leq 0.05$, 0.01, and 0.001 levels, respectively.

There were a significant year effects ($P \leq 0.05$) (Table 3-5 and 3-6) and a significant genotype x environment interaction based on F_2 data ($P \leq 0.05$), (Table 3-6). This indicates that evaluation for resistance using this component should be conducted over a number of different environments in order to obtain a reliable assessment.

Narrow Sense Heritability Estimates

Narrow sense heritability estimates were determined using the parent offspring regression analysis of F_1 on F_2 and F_2 on F_3 progeny data using the greenhouse and field tests. Narrow sense heritability estimates are shown in Table 3-19.

Narrow sense heritability values significantly different from zero indicated that differences in components of resistance are heritable. Estimates in these tests ranged from 0.0 to 0.64 for LP, 0.0 to 0.45 for LD, 0.0 to 1.27 for SP, and 0.0 to 1.20 for MPSL (Table 3-19). In the Zimbabwe tests, narrow sense heritability values were generally low. In the Florida F_1 tests, narrow sense heritability values were all significantly different from zero ($P \leq 0.05$), except for LD in 1996. This is attributed to the inconsistency of LD in rating genotypes for resistance to early leaf spot. Selection of individuals within crosses could be an effective strategy for all components of resistance except LD which could be greatly affected by environment and cross.

Table 3-19. Narrow sense heritability estimates from parent offspring regression for tests, 1990 to 1996.

Data Source	Component[1]			
	LP	LD	SP	TMPSL
F_2, 1991/92 and F_3, 1992/93 Zimbabwe.	0.13ns	0.00ns	0.00ns	0.00ns
F_2, 1992/93 and F_3, 1992/93, Zimbabwe.	0.00ns	0.07ns	0.20ns	0.14ns
F_2, 1991/92 and F_3 1993/94, Zimbabwe.	0.01ns	0.00ns	0.82**	0.00ns
F_2, 1996, Florida, and F_3, 1992/93, Zimbabwe.	0.64*	0.00ns	0.05ns	0.26ns
F_2, 1996, Florida and F_3 1992/93, Zimbabwe.	0.38ns	0.00ns	0.81ns	0.25ns
F_1, 1995 greenhouse Florida and F_2 field, 1996,	0.48**	0.45*	1.27**	1.20**
F_1, 1996 field and F_2 field, 1996, Florida.	0.52**	0.00ns	0.87**	0.89**
F_1 1995 greenhouse Florida and F_2 field 1992/93, Zimbabwe.	0.24ns	0.32ns	0.00ns	0.05ns
F_1 1995 greenhouse Florida, F_2 field 1991/92, Zimbabwe.	0.19ns	0.14ns	0.36ns	0.23ns

[1]LP=Latent period in days. LD=Lesion diameter in mm, SP=Sporulation score on 1-5 scale, TMPSL=Square root transformed maximum percentage sporulating lesions.
*, **, and ***, represent significantly different from zero at the $P \leq 0.05$, 0.01, and 0.001 levels, respectively.

Anderson et al. (3) reported narrow sense heritability values for the components of resistance to early leaf spot, lesion number, sporulation, infection rating and defoliation. They reported narrow sense heritability values ranging from 0.18 to 0.74, and concluded that selection for individual plants within crosses would be effective for some crosses but not for others. Anderson et al. (4) reported broad sense heritability values that ranged from 0.40 to 0.80 for the components lesion no/100cm^2 of leaf area, average lesion size, necrotic area, sporulation rating and latent period for both early and late leaf spot in the F_2 generation. Green and Wynne (46) reported narrow sense heritability estimates of 0.41 to 0.78 for lesion count for early leaf spot. There are no reports of heritability estimates for latent period and maximum percentage sporulating lesions for Ca in the literature.

Narrow sense heritability estimates determined by the parent offspring regression are subject to environmental effects and to genotype x environmental effects (30). They suggest regression of parent and offspring data collected from different environments to minimize the confounding effect of environment and genotype by environment effects.

Selection for individual plants among crosses could be an effective strategy but will depend on the pathosystem and the nature and magnitude of genotype x environment interactions.

CHAPTER IV
COMBINING ABILITY FOR FOUR COMPONENTS OF RESISTANCE TO EARLY LEAF SPOT OF PEANUT FROM DIFFERENT ENVIRONMENTS AND THEIR IMPLICATIONS IN BREEDING FOR RESISTANCE

Introduction

Early leaf spot, caused by *Cercospora arachidicola* Hori. (Ca), and late leaf spot, caused by *Cercosporidium personatum* [(Berk. and Curt.) Deighton.] (Cp), are major constraints to the achievement of high yields in peanut (*Arachis hypogaea* L.) (105, 116, 118). The use of disease resistant cultivars is the most sustainable and economical long term disease control.

Sources of partial resistance to early leaf spot in peanut have been identified by numerous scientists (1, 51, 65, 95, 134, 141). Resistance that has been identified is only partial and reduces the rate of the disease epidemic (45, 65). High levels of resistance have been identified in wild *Arachis* spp. Although success has been achieved in hybridizing diploid and tetraploid species, the progeny are often agronomically unsuitable and carry many undesirable characteristics (113). An understanding of the genetic control of resistance in the cultivated peanut would help transfer resistance from unadapted germplasm sources to desirable cultivars.

Kornegay et al. (71) reported general combining ability (GCA) for F_1 and F_2 generations to be significant, for disease severity rating for Ca and Cp, indicating that resistance to leaf spot disease and tolerance to infection are primarily due to additive genetic effects. Hamid et al. (49) found GCA to be five times greater than specific combining ability (SCA) for yield, fruit traits and resistance to Ca and Cp. They also found no significant reciprocal effects and concluded that nuclear genes were of primary importance. Association between yield components and leaf spot disease traits indicated that it would be possible to select for high yield and disease resistance.

Green and Wynne (44) reported GCA to be the most important but large ratios of SCA/GCA sums of squares indicated than nonadditive genetic variance was important, with epistasis being an important factor for latent period. Reciprocal effects for lesion area and lesion number/10cm^2 of lesion area were also found. Coffelt and Porter (20) found significant differences in leaf spot susceptibility between reciprocal cross populations and concluded that a cytoplasmic factor, and additive genetic effects control leaf spot disease resistance in peanut. They also concluded that higher yielding genotypes with improved resistance to leaf spot disease could be selected.

If components of resistance to Ca are under the control of additive genes or additive types of epistatic effects,

efficient selection would be facilitated. It would therefore be possible to select for improved yield and other agronomic traits as well as resistance to Ca by selecting for single progenies within crosses in early generations and make genetic gains to selection.

Few studies have reported on inheritance of resistance to Ca as rated by latent period and spore production. No studies have reported on the inheritance of resistance to Ca as rated by MPSL. This component affects the total amount of spore production and is a key factor in the development of the disease epidemic. Furthermore, if these components are under the control of different genes, more durable resistance could be built up in partially resistant cultivars (112).

The objectives of this study were: a) to determine the combining abilities for four components of resistance to Ca, b) to compare four peanut genotypes for use as parents in crosses for developing Ca resistant peanut cultivars and c) determine the best combinations among the crosses for use in a breeding program.

Materials and Methods

The genotypes and experimental procedures used in these tests are as described in Chapter III (Table 3-2). The components of resistance that were evaluated were: i) latent period (LP), ii) lesion size in mm measured as lesion diameter (LD), iii) amount of spore production using a 1 to 5 rating

scale (SP) (128), and iv) maximum percentage of sporulating lesions (MPSL), based on the number of lesions and the number of sporulating lesions on target leaves. The four peanut genotypes used in crosses were Southern Runner, Flamingo, 97-8-4, and 148-7-25.

Analysis of variance (ANOVA) was carried out for each study using entry means according to the GLM procedure of SAS (78). Analysis of variance for percentage sporulating lesions was conducted on the square root transformed values (TMPSL). Mean separation for entries was conducted using Duncan's multiple range test.

The diallel analysis procedure defined by Griffing (48) Method I, Model I was used because the parents were selected from a population. Analysis for combining ability and for reciprocal cross differences was carried out using a SAS Macro Griffing program for running Griffing Analysis of Diallel Systems, developed by Stephen B. Linda of the Institute of Food and Agricultural Sciences (IFAS) Consulting Division, Department of Statistics, University of Florida. The error degrees of freedom (df) from the ANOVA for each study were used in the SAS Macro Griffing program to generate mean squares for GCA, SCA and reciprocal effects. General combining ability effects (GCA effects), specific combining ability effects (SCA effects) and reciprocal effects were computed for each parent for four components of resistance. The relative magnitude of GCA and SCA was determined using the

ratio of GCA/SCA mean squares. For the 1992/93 F_2 test and 1993/94 F_3 test, Griffing's analysis Method II, Model I was used because two of the crosses lacked reciprocals. The expectation of mean squares for the analysis of variance for Method I Model I and Method II computed with the assumptions of Model I are presented in Table 4-1.

Results and Discussion

F_1 Generation Evaluations

The mean values for all components of resistance evaluated in the F_1 tests are presented in Tables 4-2 to 4-4. In all three F_1 tests, LP was shorter, and SP and TMPSL generally higher in the crosses that involved S. Runner as a parent (Table 4-2 to 4-4). Means for lesion diameter did not show a similar uniform trend. Progeny from crosses that involved 148-7-25, either as a male or a female, had an increased LP except for the F_1 test in the 1990/91 season. Maximum percentage sporulating lesions, however, did not always show a uniform trend. For the 1990/91 test, LP did not show this trend probably due to drought associated high environmental variance since no significant differences among entries were noted for LP in the 1990/91 test.

Diallel analysis involving parents and the F_1 was carried out on the table of means using Method I Model I (48). The sources of variation were GCA, SCA, and reciprocal effects.

Table 4-1. Generalized expectations for mean squares for analysis of variance for Griffing's Method I and II with assumptions for Model I.

Method I Model I

Source	df	Sum of squares	Mean squares	Expectations of mean squares
GCA	3	S_g	M_g	$\sigma^2 + 2.67\Sigma g_i^2$
SCA	6	S_s	M_s	$\sigma^2 + 0.17\Sigma\Sigma s_{ij}^2$
Reciprocal effects	6	S_r	M_r	$\sigma^2 + 0.33\Sigma\Sigma r_{ij}^2$
Error	m	S_e	M_e	σ^2

Method II Model I

Source	df	Sum of squares	Mean squares	Expectations of mean squares
GCA	3	S_g	M_g	$\sigma^2 + 2.0\Sigma g_i^2$
SCA	6	S_s	M_s	$\sigma^2 + 0.17\Sigma\Sigma s_{ij}^2$
Error	m	S_e	M_e	σ^2

Table 4-2. Diallel table of means for components of resistance to early leaf spot, measured in the F_1 generation for parents and crosses in the field in Zimbabwe, 1990/91.

Female	Component[1]	Male parent S. Runner	Flamingo	97-8-4	148-7-25	Row mean
S. Runner	LP	15.5	21.9	16.0	15.5	17.2
	LD	2.3d[2]	2.6bcd	2.4bcd	2.7a-d	2.5
	SP	1.5	1.4	1.3	2.3	1.6
Flamingo	LP	17.3	22.1	19.8	20.7	20.0
	LD	3.1a	2.7a-d	3.4d	2.8a-d	3.0
	SP	1.5	1.3	1.7	1.2	1.4
97-8-4	LP	20.0	21.3	25.3	17.3	21.0
	LD	2.6bcd	2.9abc	3.0ab	2.6bcd	2.8
	SP	1.7	1.4	1.6	1.4	1.5
148-7-25	LP	22.8	23.6	21.2	22.8	22.6
	LD	2.6bcd	2.4d	2.4d	2.6bcd	2.5
	SP	1.1	1.1	1.2	1.0	1.1
Mean	LP	18.9	22.2	20.6	19.1	20.2
	LD	2.7	2.7	2.8	2.4	2.7
	SP	1.5	1.3	1.0	1.5	1.3

[1]LP=latent period in days, LD=lesion diameter in mm, SP=sporulation score on a 1-5 scale, TMPSL=square root transformed maximum percentage sporulating lesions.
[2]Means followed by the same letter are not significantly different (P>0.05); parental mean values are shown in diagonal.

Table 4-3. Diallel table of means for components of resistance to early leaf spot, measured in the F_1 generation, for parents and crosses in the greenhouse in Gainesville, Florida, 1995.

Female	Component[1]	Male parent S. Runner	Flamingo	97-8-4	148-7-25	Row mean
S. Runner	LP	14.2g[2]	17.0be	16.4c-g	16.3d-g	16.0
	LD	3.3bcd	3.8abc	3.0cd	3.4a-d	3.4
	SP	2.0abc	2.1abc	1.9abc	1.8bcd	2.0
	TMPSL	6.8ab	6.2a-d	5.6a-d	6.4a-d	6.3
Flamingo	LP	16.9b-e	18.2a-e	17.5be	18.2a-e	17.7
	LD	3.6abc	3.4a-d	3.9ab	3.4a-d	3.6
	SP	2.3ab	1.7cd	1.7bcd	1.4d	1.8
	TMPSL	7.3a	5.5bcd	5.7a-d	4.9d	5.9
97-8-4	LP	14.7fg	16.1efg	18.9ab	18.7abc	17.1
	LD	3.8abc	3.3bcd	3.1d	3.2bcd	3.4
	SP	2.4a	1.7bcd	1.6cd	1.8a-d	1.9
	TMPSL	6.8abc	5.5bcd	5.5bcd	5.8a-d	5.9
148-7-25	LP	17.1b-f	18.7abc	18.9ab	20.2a	18.7
	LD	3.5a-d	4.0a	3.0cd	3.4a-d	3.5
	SP	1.7cd	1.4d	1.7cd	1.3d	1.3
	TMPSL	5.4bcd	4.6d	5.1abc	5.0cd	5.0
Mean	LP	15.7	17.5	17.5	18.4	17.3
	LD	3.6	3.6	3.3	3.4	3.4
	SP	2.1	1.7	1.8	1.6	1.8
	TMPSL	6.6	5.5	5.5	5.5	5.7

[1]LP=latent period in days, LD=lesion diameter in mm, SP=sporulation score on a 1-5 scale.
[2]Means followed by the same letter are not significantly different (P>0.05); parental mean values are shown in diagonal.

Table 4-4. Diallel table of means for components of resistance to early leaf spot, measured in the F_1 generation for parents and crosses in the field in Gainesville, Florida, 1996.

Female	Component[1]	Male parent S. Runner	Flamingo	97-8-4	148-7-25	Row mean
S. Runner	LP	12.5h[2]	14.3ef	12.9hg	13.7efg	13.4
	LD	3.2	3.4	2.9	3.3	3.2
	SP	1.6c	2.2a-e	2.2ab	1.7cd	1.9
	TMPSL	4.7ed	7.4ab	7.5ab	6.4bcd	6.5
Flamingo	LP	13.2fgh	17.3ab	16.2bcd	16.4bcd	15.8
	LD	3.3	3.7	3.3	3.4	3.4
	SP	2.2ab	1.2f	1.2f	1.3ef	1.5
	TMPSL	8.0a	5.2cde	5.5cd	4.9ed	5.9
97-8-4	LP	15.7d	16.1cd	17.9a	16.9abc	16.7
	LD	3.4	3.1	3.0	3.0	3.1
	SP	1.8bc	1.3ef	1.2f	1.5def	1.5
	TMPSL	6.6abc	5.2cde	4.9ed	5.6cd	5.6
148-7-25	LP	14.6e	17.1abc	16.2bcd	16.7a-d	16.2
	LD	3.7	3.2	3.2	3.5	3.4
	SP	2.0abc	1.2f	1.4def	1.1f	1.4
	TMPSL	7.2ab	5.6cd	5.4cde	3.8e	5.5
Mean	LP	14.0	16.2	15.8	15.9	15.5
	LD	3.4	3.4	3.1	3.3	3.3
	SP	1.9	1.5	1.5	1.4	1.6
	TMPSL	6.9	5.8	5.8	5.2	5.9

[1]LP=latent period in days, LD=lesion diameter in mm, SP=sporulation score on a 1-5 scale, TMPSL=square root transformed maximum percentage sporulating lesions.
[2]Means followed by the same letter are not significantly different (P>0.05); parental mean values are shown in diagonal.

General combining ability

For LP, SP, and TMPSL, mean squares for GCA were significant in the tests conducted in Florida ($P \leq 0.01$) (Table 4-5). Mean squares for GCA for LD were significant ($P \leq 0.05$) in 1995 and 1996 and for SP, in all three tests (Table 4-5). It can be concluded that additive genetic effects were important in the control of resistance for these components. Similar results were reported using different components of resistance (5, 49, 138).

Specific combining ability for crosses and reciprocals

Specific combining ability was significant for LP, SP, and TMPSL ($P \leq 0.001$) in the 1996 test and for LD ($P \leq 0.05$) in 1990/91 (Table 4-5). This indicates that nonadditive genetic variance was also important for these components. However, in all tests, the mean squares for GCA were generally much higher than the mean squares for SCA indicating that additive genetic variance was more important than nonadditive genetic variance in the control of resistance to Ca.

Mean squares for reciprocals were significant ($P \leq 0.01$) for LP only in the 1996 F_1 test, for LD and SP, ($P \leq 0.05$) in the 1990/91 test in Zimbabwe (Table 4-5). Although significance was not reflected in all tests, these results indicated the possible presence of a cytoplasmic factor(s) in the control of resistance to Ca. Anderson et al. (5) found reciprocal effects in the inheritance of resistance to Ca and Cp. They also reported heterosis towards the susceptible

Table 4-5. Mean squares for general combining ability (GCA) and specific combining ability (SCA) for components of resistance to early leaf spot, measured in the F_1 generation in Zimbabwe and Florida.

Source	df	Component[1] mean square			
		LP	LD	SP	TMPSL
		Zimbabwe, 1990/91			
GCA	3	16.2ns[2]	0.02ns	0.09*	-
SCA	6	5.4ns	0.06*	0.04ns	-
Reciprocal	6	9.8ns	0.07*	0.14**	-
Error	15	7.2	0.01	0.02	-
		Gainesville, Florida 1995[3]			
GCA	3	10.1***	0.14*	0.31***	2.04**
SCA	6	0.99ns	0.05ns	0.05ns	0.11ns
Reciprocal	6	0.48ns	0.12ns	0.02ns	0.38ns
Error	15	0.58	0.05	0.01	0.29
		Gainesville, Florida 1996			
GCA	3	11.80***	0.13*	0.47**	2.11***
SCA	6	0.57**	0.02ns	0.17***	2.22***
Reciprocal	6	0.88**	0.04ns	0.02ns	0.21ns
Error	15	0.14	0.03	0.01	0.22

[1]LP=latent period in days, LD=lesion diameter in mm, SP=sporulation score on a 1-5 scale, TMPSL=square root transformed maximum percentage sporulating lesions.
[2]Significance denoted by *, **, and ***, at the $P \leq 0.05$, 0.01, and 0.001 levels, respectively.
[3]The 1995 Gainesville test was conducted in the greenhouse.

parent, indicating dominance towards susceptibility. Reciprocal effects for leaf spot disease parameters were reported (20, 44, 49). However, Hamid et al. (49) observed no maternal effects or reciprocal effects for fruit and leaf spot resistance traits.

GCA effects

The means in tables 4-2 and 4-5 were used to calculate the GCA effect for each parent. The GCA effect of a parent is a measure of its relative importance in a cross combination. The larger the GCA effect, the better is the parent at transmitting its phenotype to its progeny. In a breeding program to develop resistance to Ca, it is desirable to have a parent with high levels of components of resistance and good ability to transmit its phenotype to progeny. For latent period, a large positive GCA effect is more desirable. For lesion diameter, sporulation score and maximum percentage sporulating lesions, a large negative GCA effect is the desired effect.

Values for GCA effects for the four components of resistance are shown in Table 4-6. Student's T test was used to test whether the GCA effects are different from zero. In the 1996 test GCA effects for LP and SP for Southern Runner were significantly different from zero (Table 4-6). Values for GCA effects were -1.52 for LP and 0.36 for SP, this means that Southern Runner had a marked effect in reducing the latent period and increasing the amount of spore production

Table 4-6. Estimates of general combining ability (GCA) effects for components of resistance to early leaf spot, measured in the F_1 generation in Zimbabwe and Florida.

Parent	Components[1] LP	LD	SP	TMPSL
	Zimbabwe, 1990/91			
S. Runner	-2.12[2]	-0.04	0.11	-
Flamingo	0.90	0.05	-0.06	-
97-8-4	0.58	0.03	0.06	-
148-7-25	0.64	-0.03	-0.11	-
SE± =	1.18	0.18	0.13	-
	Florida, 1995[3]			
S. Runner	-1.54	0.01	0.24	0.69
Flamingo	0.24	0.17	-0.04	-0.07
97-8-4	0.14	-0.12	0.03	-0.10
148-7-25	0.47	-0.10	-0.10	-0.30
SE ± =	0.47	0.14	0.11	0.33
	Florida, 1996			
S. Runner	-1.52*[4]	0.01	0.36*[4]	0.69
Flamingo	0.50	0.10	-0.09	0.03
97-8-4	0.74	-0.18	-0.10	-0.20
148-7-25	0.56	0.08	-0.17	-0.52
SE ± =	0.28	0.13	0.09	0.36

[1]LP=latent period in days, LD=lesion diameter in mm, SP=sporulation score on a 1-5 scale, TMPSL=square root transformed maximum percentage sporulating lesions.
[2]Values not significantly different from zero ($P>0.05$).
[3]The 1995 Gainesville test was conducted in the greenhouse.
[4]Values were significantly different from zero at the ($P\leq0.05$) level.

among progeny. All other GCA effects were not significantly different from zero.

Although GCA values were not significantly different from zero, the parent, 148-7-5, gave the highest positive GCA effect for LP in the 1995 test and 97-8-4 had the highest positive GCA effect in the 1996 F_1 test in Florida (Table 4-6). The GCA effects for lesion diameter for the four parents were generally small, indicating that the effect of the parents on the progeny on lesion diameter was small. Southern Runner, consistently had the largest positive effect on TMPSL in all seasons. Southern Runner therefore generally increased susceptibility of progeny in all tests by increasing the maximum percentage of sporulating lesions. The parent 148-7-25 had the largest effect of reducing the amount of spore production in 1990 and the maximum percentage sporulating lesions in 1995 and 1996. In general, 148-7-25 had a more consistent effect of increasing LP, decreasing SP and TMPSL in all three F_1 tests and was more consistent than 97-8-4 and Flamingo.

SCA effects for crosses and reciprocals

Specific combining ability effects were calculated for all four components according to Hayman (53). These were used to evaluate the role of dominance in the inheritance of components of resistance. Large SCA variances compared to GCA variances indicate a large influence of dominance in the inheritance of components of resistance. A good parent is one

that has a combination of SCA effects that reflect high positive values for LP, and high negative values for LD, SP and TMPSL. Estimates of SCA effects for the F_1 test of 1990/91 and in Zimbabwe the 1995 test in Florida were not significantly different from zero ($P>0.05$) and are presented in Appendix D, and F, respectively.

The SCA effects for the F_1 test in 1996 are presented in Table 4-7. One reciprocal cross, 97-8-4 x Southern Runner had a SCA effect of 1.37 for LP, which was significantly different from zero ($P\leq0.001$) in 1996 (Table 4-7). It appears that 97-8-4, when used as a female with Southern Runner resulted in an increased LP. Although Southern Runner had a noted effect of reduction of LP among its progeny in general, this cross resulted in progeny with a generally higher LP.

F_2 Generation Evaluations

The diallel table of means for all F_2 tests conducted are shown in Tables 4-8 to 4-10. Means for a given component followed by the same letter are not significantly different at the ($P\leq0.05$) level. Crosses involving Southern Runner generally had shorter latent periods, more spore production and a higher maximum percentage of sporulating lesions (Table 4-8 to 4-10). For lesion diameter, however this trend did not show consistently. The observed patterns for LP, SP, and TMPSL were similar to the observations made in the F_1 test. For all components, there was no cross significantly better

Table 4-7. Estimates of specific combining ability (SCA) effects for components of resistance to early leaf spot, measured in the F_1 generation in the field in Gainesville, Florida, 1996.

Female	Component[1]	Male parent: S. Runner	Flamingo	97-8-4	148-7-25
S. Runner	LP	-	-0.45	-0.11	-0.10
	LD	-	-0.03	0.01	0.11
	SP	-	0.37	0.22	0.07
	TMPSL	-	1.13	0.66	0.74
Flamingo	LP	-0.54	-	-0.60	0.19
	LD	0.04	-	-0.05	-0.14
	SP	0.04	-	-0.13	-0.04
	TMPSL	-0.24	-	-0.39	-0.09
97-8-4	LP	1.37***[2]	-0.04	-	-0.24
	LD	0.23	-0.10	-	-0.04
	SP	-0.22	0.06	-	0.12
	TMPSL	-0.44	0.14	-	0.36
148-7-25	LP	0.46	0.35	-0.38	-
	LD	0.18	-0.10	0.10	-
	SP	0.13	-0.02	-0.04	-
	TMPSL	0.43	0.35	-0.10	-

S.E.	s_{ij}[3]	S.E.	r_{ij}[4]
LP	$\pm$ 0.51	LP	$\pm$ 0.28
LD	$\pm$ 0.08	LD	$\pm$ 0.13
SP	$\pm$ 0.16	SP	$\pm$ 0.09
TMPSL	$\pm$ 0.65	TMPSL	$\pm$ 0.35

[1]LP=latent period in days, LD=lesion diameter in mm, SP=sporulation score on a 1-5 scale, TMPSL=square root transformed maximum percentage sporulating lesions.
[2]Significantly different from zero at the P<0.001 levels.
[3]Standard error of SCA effects for crosses.
[4]Standard error of SCA effects for reciprocals.

Table 4-8. Diallel table of means for components of resistance to early leaf spot, measured in the F_2 field test for parents and crosses at Gwebi, Zimbabwe, 1991/92.

Female	Component[1]	Male parent S. Runner	Flamingo	97-8-4	148-7-25	Row mean
S. Runner	LP	20.0bcd[2]	24.2abc	19.0cd	17.2d	20.1
	LD	2.0	2.1	2.0	2.3	2.1
	SP	2.1	2.0	2.0	2.2	1.6
	TMPSL	7.0a	5.9abc	6.0abc	7.0a	6.4
Flamingo	LP	23.8a-d	24.4abc	27.3a	26.5a	25.5
	LD	2.1	2.9	2.0	2.6	2.4
	SP	2.0	2.0	2.0	2.00	1.6
	TMPSL	6.5ab	4.0c	7.0a	7.0a	6.1
97-8-4	LP	25.1abc	24.1abc	29.0a	24.4abc	25.7
	LD	1.9	2.1	2.1	2.2	2.3
	SP	2.0	2.0	2.1	2.0	1.6
	TMPSL	5.9abc	7.0a	7.7a	7.4a	7.0
148-7-25	LP	27.0a	25.4abc	26.2ab	25.0abc	25.9
	LD	2.3	2.1	2.3	2.1	2.2
	SP	2.0	1.9	2.0	2.0	1.4
	TMPSL	6.6a	5.7abc	4.5bc	5.7abc	5.6
Mean	LP	24.0	24.5	25.4	25.3	24.4
	LD	2.1	2.3	2.1	2.3	2.2
	SP	1.9	1.3	1.6	1.6	1.6
	TMPSL	6.5	5.7	6.3	6.8	6.4

[1]LP=latent period in days, LD=lesion diameter in mm, SP=sporulation score on a 1-5 scale, TMPSL=square root transformed maximum percentage sporulating lesions.
[2]Means followed by the same letter are not significantly different (P>0.05); parental mean values are shown in diagonal.

Table 4-9. Diallel table of means for components of resistance to early leaf spot, measured on the F_2 generation for parents and crosses in the field, Gainesville, Florida, 1996.

Female	Component[1]	Male parent S. Runner	Flamingo	97-8-4	148-7-25	Row mean
S. Runner	LP	12.4f[2]	12.8fe	13.8c-f	13.5def	13.1
	LD	3.3	3.0	3.4	3.0	3.2
	SP	2.8a	2.3bcd	1.9c-f	1.9b-e	2.2
	TMPSL	7.7ab	6.8bcd	7.3abc	6.8bcd	7.2
Flamingo	LP	14.0c-f	15.2b-e	15.4b-e	14.8b-f	14.9
	LD	3.4	3.6	3.9	3.2	3.5
	SP	2.5ab	1.3e-h	1.4e-h	1.3fgh	1.6
	TMPSL	8.0ab	5.1ef	5.7def	5.4ef	6.1
97-8-4	LP	14.4c-f	14.2c-f	15.8a	15.8a-d	15.1
	LD	3.4	3.3	3.0	3.3	3.3
	SP	2.4abc	1.5e-h	1.6efg	1.4e-h	1.7
	TMPSL	8.2a	6.0c-f	5.5ef	5.4f	6.3
148-7-25	LP	16.0a-d	16.4abc	18.1b-e	17.3ab	17.0
	LD	3.3	3.5	3.0	3.4	3.3
	SP	1.7d-g	1.3fgh	1.1h	1.2gh	1.3
	TMPSL	6.8b-e	4.9f	4.9f	5.2f	5.5
Mean	LP	14.2	14.7	15.8	15.4	15.0
	LD	3.3	3.4	3.3	3.2	3.3
	SP	2.4	1.6	1.5	1.5	1.8
	TMPSL	7.9	5.7	5.9	5.7	6.3

[1]LP=latent period in days, LD=lesion diameter in mm, SP=sporulation score on a 1-5 scale, TMPSL=square root transformed maximum percentage sporulating lesions.
[2]Means followed by the same letter are not significantly different (P>0.05); parental mean values are shown in diagonal.

Table 4-10. Diallel table of means for components of resistance to early leaf spot, measured on the F_2 generation for parents and crosses in the field, in Zimbabwe, 1992/93.

Female	Component[1]	Male parent S. Runner	Flamingo	97-8-4	148-7-25	Row mean
S. Runner	LP	14.00e[2]	16.0abc	17.7cde	14.0e	14.7
	LD	2.4cd	2.9abc	3.2a	2.1d	2.5
	SP	2.3	2.0	2.1	2.5	2.3
	TMPSL	5.7ab	4.6abc	4.5bc	5.8a	5.4
Flamingo	LP	-	15.3bcd	15.0b-e	17.0a	15.5
	LD	-	3.1ab	3.1ab	3.0abc	3.1
	SP	-	2.0	2.2	2.3	2.2
	TMPSL	-	5.1abc	4.8abc	4.9abc	4.8
97-8-4	LP	15.3	-	14.3ed	14.5ed	14.7
	LD	3.1ab	-	3.4a	2.6bcd	3.0
	SP	2.1	-	2.0	1.9	2.0
	TMPSL	5.1abc	-	4.6abc	4.5c	4.7
148-7-25	LP	14.8cde	15.9	16.2ab	16.7a	15.9
	LD	3.2a	3.0abc	3.0abc	3.0ab	3.1
	SP	2.1	2.0	1.8	2.0	2.0
	TMPSL	4.4c	5.0abc	4.7abc	4.6abc	4.9
Mean	LP	14.7	15.6	15.4	15.6	15.2
	LD	3.0	3.1	3.1	2.7	3.0
	SP	2.2	2.0	2.0	2.2	2.1
	TMPSL	4.9	5.1	4.7	5.0	5.0

[1]LP=latent period in days, LD=lesion diameter in mm, SP=sporulation score on a 1-5 scale, TMPSL=square root transformed maximum percentage sporulating lesions.
[2]Means followed by the same letter are not significantly different (P>0.05); parental mean values are shown in diagonal.

than the better parent. Diallel analysis involving the parents and the F_2, was carried out on the table of means using Method I, Model I (48) for the 1991/92 and 1996 tests. For the 1992/93 test, Method II with the assumptions of Model I was used because two of the crosses lacked reciprocals. Griffing's model II precludes reciprocals in the analysis.

General combining ability

The mean squares from Griffing's combining ability analyses are shown in Table 4-11. Mean squares for GCA were significant for LP ($P \leq 0.01$) in all tests for F_2 data. For LD, GCA was only significant ($P \leq 0.01$) in the 1992/93 test in Zimbabwe. The GCA mean square for TMPSL, and SP was significant ($P \leq 0.01$) only in the 1996 F_2 test in Florida. This indicates that additive genetic effects were important in the inheritance of LP, SP, and TMPSL. The GCA variance was also much greater than the SCA variance in all the F_2 tests. This result is similar to the observation made in the F_1 tests and supports the conclusion that additive genetic effects are more important than nonadditive genetic effects.

Mean square for GCA for LD was significant ($P \leq 0.01$) for the 1992/93 test (Table 4-11). The magnitude of the GCA MS for the components were much higher than the MS for SCA. Although LD was an inconsistent component, these results indicate that lesion size is under the control of additive genetic effects.

Table 4-11. Mean squares for general combining ability (GCA) and specific combining ability (SCA) for components of resistance to early leaf spot, measured in the F_2 generation in the field in Gainesville, Florida and at Gwebi, Zimbabwe.

		Component[1]			
		LP	LD	SP	TMPSL
		Zimbabwe, 1991/92			
GCA	3	20.90**[2]	0.11ns	0.14ns	0.89ns
SCA	6	2.54ns	0.07ns	0.03ns	1.24**
Reciprocal	6	12.85**	0.02ns	0.10ns	0.90*
Error	28	4.48	0.05	0.06	0.34
		Zimbabwe, 1992/93			
GCA	3	1.37***	0.23**	0.04ns	0.30ns
SCA	6	1.04***	0.10***	0.03ns	0.17ns
Error	15	0.13	0.02	0.02	0.12
		Florida, 1996			
GCA	3	7.92***	0.11ns	1.17***	5.36***
SCA	6	1.01ns	0.06ns	0.02ns	0.35ns
Reciprocal	6	0.92ns	0.04ns	0.04ns	0.25ns
Error	15	0.60	0.05	0.03	0.16

[1]LP=latent period in days, LD=lesion diameter in mm, SP=sporulation score on a 1-5 scale, TMPSL=square root transformed maximum percentage sporulating lesions.
[2]Significance denoted by *, **, and ***, at the $P \leq 0.05$, 0.01, and 0.001 levels, respectively.

Specific combining ability for crosses and reciprocals

Specific combining ability was not significant for any components in 1996, but was significant ($P \leq 0.001$) for LP and LD in the 1992/93 test and for TMPSL in the 1991/92 test (Table 4-11). For these components, nonadditive genetic effects were also important. In the majority of cases, the MS due to GCA was higher than that the MS for SCA.

The mean square for reciprocals for LP was significant ($P \leq 0.01$) in the 1991/92 and for TMPSL ($P \leq 0.05$) (Table 4-11). Significant MS for reciprocals were also noted for LP in the F_1 test in 1996 and for TMPSL in the 1990/91 F_1 test. These results indicated a possible cytoplasmic factor involved in the inheritance of resistance to Ca, as reported by Coffelt and Porter (20). The MS for GCA for most components was larger than the MS for reciprocal effects, indicating that additive genetic effects are more important than nonadditive effects.

GCA effects

Means for parental lines computed over crosses (Tables 4-8 to 4-10) were used to calculate GCA effects for each parent. The values for GCA effects are presented in (Table 4-12). The GCA effects for SP and TMPSL were significantly different from zero for Southern Runner in 1996 (Table 4-12). This indicates that this parent had a marked influence on the progeny of increasing the amount of spore production and the maximum percentage sporulating lesions. Southern Runner also had the

Table 4-12. Estimates of general combining ability (GCA) for components of resistance to early leaf spot, measured in the F_2 generation in Florida and Zimbabwe.

Parent	Component[1]			
	LP	LD	SP	TMPSL
	Zimbabwe, 1991/92			
S. Runner	-2.34[2]	-0.19	0.18	0.19
Flamingo	0.89	0.14	-0.13	-0.42
97-8-4	1.22	-0.09	0.02	0.33
148-7-25	0.23	0.04	-0.07	-0.11
S E ± =	1.09	0.12	0.12	0.31
	Zimbabwe, 1992/93			
S. Runner	-0.52	-0.19	0.18	0.30
Flamingo	0.27	0.17	0.00	-0.03
97-8-4	0.26	0.16	-0.10	-0.24
148-7-25	0.52	-0.10	0.03	-0.03
S E ± =	0.53	0.23	0.21	0.47
	Florida 1996[3]			
S. Runner	-1.33	-0.03	0.55*[4]	1.19*[4]
Flamingo	-0.19	0.11	-0.11	-0.36
97-8-4	0.72	-0.04	-0.11	-0.18
148-7-25	0.80	0.13	-0.09	-0.35
S E ± =	0.47	0.21	0.10	0.32

[1]LP=latent period in days, LD=lesion diameter in mm, SP=sporulation score on a 1-5 scale, TMPSL=square root transformed maximum percentage sporulating lesions.
[2]Not significantly different from zero at the ($P \leq 0.05$).
[3]Test conducted in greenhouse.
[4]Significantly different from zero at the $P \leq 0.05$ level.

largest negative effect on LP of -2.34 in the 1991/92 test and -1.33 in the 1996 test (Table 4-12). The GCA effects for 148-7-25 for LP, ranged from 0.23 in 1991/92 to 0.80 in 1996, while those for 97-8-4 ranged from 0.26 to 1.22. The parent 97-8-4 had a high positive GCA effect for LP and low or negative GCA effects for LD, SP and TMPSL. For lesion diameter, GCA effects were generally low, which was similar to that obtained in the F_1 tests.

In two of the tests, 1992/93 and 1996, the genotype 148-7-25 had the highest positive GCA effect for latent period (Table 4-12). In all seasons, Southern Runner had a negative GCA effect for LP, which was always the lowest among the parents. This indicates that Southern Runner, always tended to reduce the latent period among its progeny. This is consistent with the previous observations that progeny in which Southern Runner was involved generally had shorter LP values. The parent 148-7-25 and Flamingo gave the largest negative values for GCA effects for TMPSL, -0.35 and -0.42, respectively (Table 4-12) although they were not significantly different from the other parents. For SP, Flamingo had the highest negative GCA effect of -0.13, while Southern Runner had the highest positive value of 0.55. Based on these observations, the parent 148-7-25 was better than Flamingo but was closely comparable to 97-8-4.

SCA effects for crosses and reciprocals

The SCA effects for crosses and reciprocals for the 1996, 1991/92, and 1992/93 tests were not significantly different from zero, and are presented in Appendix E, G, and H respectively.

F_3 Generation Evaluations

The mean values for the four components of resistance for F_3 tests are presented in Tables 4-13 and 4-14. No data are presented for the cross Flamingo x Southern Runner, since no viable F_1 seed were recovered from the cross. The cross of 97-8-4 x Flamingo yielded no F_2 seed due to drought in the 1991/92 season. Progeny from Southern Runner crosses often had a shorter LP (Table 4-13). This was, however, not clearly expressed in the 1993/94 test due to the low range in LP among entries that was noted for that season. There were no significant differences detected among entries for SP in this test (Table 4-13).

There were significant differences among entries for LD (Table 4-13 and 4-14). Southern Runner had the most spore production with a mean sporulation score of 2.2 compared to 148-7-25 with a mean score of 1.3 in 1993/94 (Table 4-14). The effect of the parents 97-8-4, Flamingo, and 148-7-25 was to reduce the level of spore production among the progeny (Table 4-14). However, the crosses themselves did not differ markedly in the amount of spore production. Maximum

Table 4-13. Diallel table of means for components of resistance to early leaf spot, measured in the F_3 generation for parents and crosses in Zimbabwe, 1992/93.

Female	Component[1]	Male Parent S. Runner	Flamingo	97-8-4	148-7-25	Row mean
S. Runner	LP	14.4g[2]	16.7de	15.2fg	16.1fe	15.6
	LD	3.0bcd	3.2abc	2.8d	3.1bcd	3.0
	SP	2.1	2.0	2.0	2.2	2.1
	TMPSL	6.7abc	5.6cde	6.6abc	6.6abc	6.4
Flamingo	LP	16.6de	18.2abc	18.0a-d	17.1cde	17.5
	LD	3.0cd	3.5a	3.2bcd	3.2bcd	3.2
	SP	2.0	2.0	2.0	2.0	2.0
	TMPSL	6.8abc	5.7be	6.3a-d	6.4a-d	6.3
97-8-4	LP	19.2a	18.5abc	17.4b-e	18.7ab	18.5
	LD	3.0bcd	3.3abc	3.2bc	3.2	3.2
	SP	2.0	2.0	2.1	2.0	2.0
	TMPSL	6.9ab	6.5a-d	7.2a	7.2a	7.0
148-7-25	LP	17.9a-d	17.7a-d	18.3abc	18.0a-d	18.0
	LD	3.3ab	3.2abc	3.2bc	3.3abc	3.3
	SP	2.0	1.9	2.0	2.0	2.0
	TMPSL	5.5cde	4.9e	5.3de	5.2e	5.2
Mean	LP	17.0	17.7	17.2	17.5	17.4
	LD	3.1	3.3	3.1	3.2	3.2
	SP	2.0	2.0	2.0	2.1	2.0
	TMPSL	6.5	5.7	6.4	6.4	6.2

[1]LP=latent period in days, LD=lesion diameter in mm, SP=sporulation score on a 1-5 scale, TMPSL=square root transformed maximum percentage sporulating lesions.
[2]Means followed by the same letter are not significantly different (P>0.05); parental mean values are shown in diagonal.

Table 4-14. Diallel table of means for components of resistance to early leaf spot, measured in the F_1 generation for parents and crosses in Zimbabwe, 1993/94.

Female	Component[1]	Male Parent S. Runner	Flamingo	97-8-4	148-7-25	Row mean
S. Runner	LP	18.1ed[2]	21.2ab	21.0abc	18.1ed	19.1
	LD	3.2bcd	3.0cd	2.9d	3.0cd	3.0
	SP	2.2a	1.4bc	1.4bc	1.9ab	1.4
	TMPSL	7.1ab	6.5abc	6.4bc	7.2a	6.9
Flamingo	LP	-	20.9abc	19.8bcd	19.5bcd	20.4
	LD	-	3.1cd	3.4a-d	3.7ab	3.3
	SP	-	1.4bc	1.2c	1.3c	1.3
	TMPSL	-	6.0abc	5.7bcd	6.2abc	6.1
97-8-4	LP	21.0abc	-	20.8abc	21.6a	21.1
	LD	3.2bcd	-	3.2bcd	3.1cd	3.2
	SP	1.4bc	-	1.4bc	1.2c	1.3
	TMPSL	6.2abc	-	6.5abc	6.4d	6.4
148-7-25	LP	19.7bcd	20.5abc	19.3cd	19.7bcd	19.8
	LD	3.5abc	3.3a-d	3.7ab	3.8a	3.6
	SP	1.4bc	1.4bc	1.5bc	1.3c	1.4
	TMPSL	5.8abc	5.8abc	5.0ad	5.5cd	5.5
Mean	LP	20.0	20.7	20.2	19.7	20.1
	LD	3.2	3.2	3.3	3.4	3.3
	SP	1.6	1.4	1.4	1.1	1.5
	TMPSL	6.4	5.9	5.9	6.3	6.2

[1]LP=latent period in days, LD=lesion diameter in mm, SP=sporulation score on a 1-5 scale, TMPSL=square root transformed maximum percentage sporulating lesions.
[2]Means followed by the same letter are not significantly different (P>0.05); parental mean values are shown in diagonal.

percentage sporulating lesions showed a similar trend (Table 4-13 to 4-14). The best crosses for any components often were only as good as the best parent used in the cross.

Diallel analysis involving the parents and the F_3 was carried out on the tables of means using Method I, Model I, for the 1992/93 test. Method II, Model I, was used for the 1993/94 test because two of the crosses lacked reciprocals.

General combining ability

Mean squares for GCA, SCA, and reciprocals are presented in Table 4-15. Mean squares for GCA for all components were significant in both tests ($P \leq 0.05$), except for SP in the 1992/93 test (Table 4-15). This result generally agrees with observations made in the F_2 and F_1 tests. Mean squares due to GCA were in all cases larger than mean squares due to SCA. This reinforces the conclusion that resistance due to these components is under the control of additive genetic effects.

Specific combining ability for crosses and reciprocals

Significant SCA ($P \leq 0.05$) were noted for LP in the two F_3 tests but only in the 1993/94 test for LD (Table 4-15). Significant SCA effects were also found for LP in the F_1 and F_2 tests, indicating that nonadditive genetic effects are also important in the genetic control of LP. Mean squares for reciprocals were significant ($P \leq 0.01$) for LP and TMPSL in the 1992/93 test (Table 4-15). A similar result was noted for LP in the F_2 test in 1996 and in 1991/92 tests and for LD in the 1990/91 test. Reciprocal effects indicate the possible

Table 4-15. Mean squares for general combining ability (GCA) and specific combining ability (SCA) for components of resistance to early leaf spot, measured in the F_3 generation in Zimbabwe, 1992/93 and 1993/94.

Source	df	Component[1] mean square			
		LP	LD	SP	TMPSL
		Zimbabwe, 1992/93			
GCA	3	4.11***[2]	0.06***	0.007ns	1.29***
SCA	6	0.47*	0.02ns	0.004ns	0.02ns
Reciprocal	6	1.66***	0.02ns	0.004ns	0.71**
Error	43	0.20	0.01	0.005	0.14
		Zimbabwe, 1993/94			
GCA	3	1.91*	0.13**	0.22**	0.70***
SCA	6	1.36***	0.07**	0.04ns	0.24ns
Error	15	0.19	0.02	0.02	0.10

[1]LP=latent period in days, LD=lesion diameter in mm, SP=sporulation score on a 1-5 scale, TMPSL=square root transformed maximum percentage sporulating lesions.
[2]Significance denoted by *, **, and ***, at the $P \leq 0.05$, 0.01, and 0.001 levels, respectively.

presence of a cytoplasmic factor in the genetic control of resistance.

Nonadditive genetic effects could be important in the control of latent period, lesion diameter, amount of sporulation and maximum percentage sporulating lesions. However, variance due to GCA was generally much higher than variance due to SCA, indicating that control of resistance is largely due to additive genetic effects.

GCA effects

None of the GCA effects for the four components of resistance to Ca for F_3 data were significantly different from zero and are presented in Appendix I. Southern Runner had a negative GCA effect for latent period in both tests with values of -0.64 and -1.07 (Appendix I). The GCA effects for SP, TMPSL, and LD were generally low and close to zero. The parent 97-8-4 had the largest positive GCA effect on LP of 0.59 in 1993/94 (Appendix I).

SCA effects for crosses and reciprocals

The SCA effects for crosses and reciprocals were not significantly different from zero and are shown in Appendix J and K, respectively, for the 1993/93 and 1993/94 tests. SCA effects for LD were noted to be generally low and close to zero. This was also observed in both the F_1 and F_2 tests. Lesion diameter is of limited use in selecting genotypes for use to make crosses to develop resistance to Ca due to the low apparent heritability of the trait. In the 1993/94 test, the

best cross which gave a large positive effect on LP and large negative effects on LD, SP, and TMPSL was 97-8-4 and 148-7-25.

Proportion of Mean Square of GCA to SCA

The magnitude of the proportion of GCA to SCA is an indicator of the relative importance of additive versus nonadditive forms of genetic variation in the control of resistance. If the ratio of GCA to SCA is greater than 1, this indicates that additive genetic effects are more important in the control of resistance than nonadditive genetic effects. Ratios of GCA to SCA that are less than 1 indicate that nonadditive genetic effects are more important than additive genetic effects.

The ratios of MS for GCA to SCA were calculated for the F_1, F_2, and F_3 tests for the different tests. The computed ratios were then pooled over seasons within generations and the results are presented in Table 4-16.

In general, GCA was significant for most traits in most seasons. Specific combining ability was significant for some components in some of the tests. The ratio of GCA to SCA ranged from 5 to 12 for latent period, was 2 to 3 times for lesion diameter, was 4 to 21 for SP, and was 6 to 34 for TMPSL (Table 4-16). It can be concluded that additive genetic effects are more important than nonadditive gene effects in the control of partial resistance, as measured by these four components of resistance. Partial resistance is therefore

Table 4-16. Proportion of mean squares (MS) of GCA to SCA for components of resistance to early leaf spot, measured on different, generations and pooled over different environments.

Component[1]	Generation		
	F_1	F_2	F_3
LP	11.6	6.1	5.1
LD	3.2	1.6	2.4
SP	3.7	21.4	3.6
TMPSL	8.7	5.9	33.7

[1]LP=latent period in days, LD=lesion diameter in mm, SP=sporulation score on a 1-5 scale, TMPSL=square root transformed maximum percentage sporulating lesions.

controlled by multiple genes in a quantitative manner. Green and Wynne (45) found additive genetic variance to be the most important in the inheritance of components of resistance to early leaf spot. They also found evidence of epistatic gene action for latent period. Hamid et al. (49) reported GCA variance to be 2 to 5 times greater than SCA for yield, fruit traits and leaf spot resistance. Walls and Wynne (138) reported GCA variances of 5 to 10 times greater than SCA variances for lesion area, defoliation and latent period. Chiyembekeza (16) reported GCA/SCA ratios ranging from 4 to 11 for latent period, 2 to 9 for lesion diameter and 11 to 21 for spore production for late leaf spot.

In breeding for resistance to Ca, the use of components of resistance, LP, LD, SP, and TMPSL, is useful tool because these traits show heritable variation. Additive genetic effects are more important than nonadditive genetic effects. Selection of individual plants within crosses using components of resistance should lead to genetic advance in levels of resistance. The magnitude of the GCA variance however was not constant from one environment to another. It is therefore important to establish the levels of heritability attainable in a given environment before establishing a long term program to develop resistant cultivars using components of resistance to Ca.

Although LD was found to be under genetic control, mainly additive genetic effects, the transmissibility of this

trait to progeny was consistently low for all parents. It would not be effective to use LD as the sole criterion in rating components for partial resistance to Ca. Latent period was the component with the largest and most consistent GCA effects among the parents.

CHAPTER V

ASSOCIATIONS AMONG COMPONENTS OF RESISTANCE TO EARLY LEAF SPOT IN PEANUT (*ARACHIS HYPOGAEA* L.) WITHIN AND BETWEEN DIFFERENT ENVIRONMENTS

Introduction

Early and late leaf spot, caused by *Cercospora arachidicola* Hori. (Ca) and late leaf spot caused by *Cercosporidium personatum* [(Berk. & Curt.) Deighton.] (Cp) are important diseases that cause reduced yields in peanuts wherever they are grown. They can be controlled successfully using fungicides (94, 108, 110, 117).

The use of disease resistant cultivars is the most economical long term strategy for the control of early leaf spot (70, 92, 105, 143). No sources of single gene immunity have been identified in the cultivated peanut (*Arachis hypogaea* L.) (71, 105). Sources of resistance have been identified by numerous scientists (1, 51, 136). The resistance identified is only partial and has been attributed to a number of components that are rate reducing (4, 45, 65, 88, 100, 135).

Progress in developing resistant cultivars depends on the levels of the components, the strengths of the components in reducing the rate of development of the epidemic under field conditions, the ease with which they can be evaluated, and the

magnitude of the environmental effects on expression of the components. Some of the components of resistance are strongly associated with one another but the association is not complete (45, 88, 135).

Components of rate reducing resistance, latent period, spore production and time to leaflet defoliation, were more highly correlated with area under disease progress curves (AUDPC's) than infection and defoliation rates (65). In these tests, maximum percentage sporulating lesions was the most highly correlated with AUDPC. Aquino et al. (7) reported a high correlation between AUDPC and maximum percentage sporulating lesions (MPSL) for Cp. If components are strongly associated, selection for resistance using one component would simultaneously improve other components of resistance.

Relationships among various components of resistance to Ca have been determined in specific environments (3, 45, 65, 88, 100, 135). Green and Wynne (45) determined the relationships among components of resistance to Ca. They reported significant rank correlations between field and greenhouse measurements for some components.

It would be useful to determine how the consistency of the associations among components vary when measured in different environments. Levels and stability of components of resistance have been reported to vary with changes in environmental factors such as temperature (133). Some germplasm lines reported to be resistant to Ca in the USA were

reported to be susceptible in India and in Malawi (92, 137) and other genotypes found to be resistant to Ca in India were reported to be susceptible in West Africa (136). These differential reactions may be due to different physiological races of Ca prevalent in the different areas. Subba Rao et al. (126) found isolate differences in symptom characters, infection frequency, and lesion size for Ca. Such variations would be expected to impact on a breeding program for development of early leaf spot resistant genotypes.

Under field conditions, evaluations of genotypes for resistance to leaf spot diseases is often done using a field plant appearance score (PAS) rating scale such as the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) 1-9 or the Florida 1-10 scales to rate genotypes for partial resistance. These are faster than the determinations of single components of rate reducing resistance when large numbers of genotypes are involved under field conditions. The association between the PAS ratings and components of resistance to Cp have been determined (126). The consistency of this association under different environmental conditions however has not been determined for Ca.

The objectives of this study were to a) determine the phenotypic correlation among components of resistance within and among different environments, b) study the stability of four components of resistance measured in diverse

environments, c) determine the relationship between the Ca pathogen isolates from diverse environments.

Materials and Methods

The genotypes used in these tests consisted of four genotypes and 12 crosses derived from full diallel crosses among them. The levels of four components of resistance were estimated during the seasons 1990/91 to 1993/94 in Zimbabwe and 1995 and 1996 in Florida. The components of resistance were latent period (LP), lesion diameter (LD), amount of spore production (SP), and maximum percentage sporulating lesions (analyzed as the square root transformed percentage sporulating lesions) (TMPSL). Definitions of the components and details of the different tests and procedures of data collection are presented in Chapter III.

In addition, in some field tests, the plants were rated for the level of early leaf spot disease using the Florida plant appearance score (PAS) rating on a 1-10 scale (14). Ratings were done at 120 days after planting (DAP) (PAS1) and at 145 DAP (PAS2). In the F_1 and F_2 tests in Florida, the relative prevalence of Ca and Cp was compared by counting lesions (LC), of Ca and Cp on ten leaf samples collected from each of ten randomly selected plants per plot at 120 and 145 DAP. Leaves were sampled from the third to fifth nodes from the growing point on the main stem.

Statistical Analysis

Analysis of variance was conducted on PAS and on the square root transformed lesion counts per ten leaves. Lesion counts per leaf were transformed using the square root transformation, where transformed lesion count=$(LC)^{1/2}$.

The associations among components of resistance and PAS within tests were determined using Pearson's correlation analysis (123). The correlation coefficient r, was determined by the relationship: $r_{xy}=Cov_{xy}/(V_xV_y)^{1/2}$, where r=correlation coefficient between two components; x and y represent two different components; Cov_{xy}=covariance of x and y, V_x=variance of the means of component x, and V_y=variance of the means of component y. Correlation analysis was carried out in those tests where two or more components showed significant differences at the $P\leq 0.05$ level.

To determine the relationships between measurements of components in different environments, Kendall's tau β rank correlation coefficient (57) was used, which adjusts for possible ties among genotype means for each variable. In all cases correlations were computed only for those tests in which two or more components showed significant differences at the ($P\leq 0.05$) level.

Results and Discussion

Early and Late Leaf Spot Lesion Counts

The results of analysis of variance on lesion counts (LC) for early leaf spot (Ca) and late leaf spot (Cp) over two dates in the F_2 test in Gainesville are shown in Table 5-1 and 5-2. The date x genotype interaction mean square was used to test for significance of the mean squares for replicates, entries and dates. The error mean square was used to test for significance of the mean square for date x genotype interaction.

The date x genotype interaction was not significant ($P \leq 0.05$) for Ca and Cp (Table 5-1). There were significant differences between dates ($P \leq 0.05$) for Ca and Cp. This reflects the increase in disease levels as the disease progressed from 120 to 145 DAP. Means for lesion counts within dates are presented in Table 5-3. There were significant differences among entries ($P \leq 0.01$) for Cp at 120 DAP but not at 145 DAP (Table 5-2). For Ca, there were no significant differences among entries ($P > 0.05$) on either date. The parents 148/7/25 and Flamingo had significantly lower Cp lesion counts than 97-8-4 and Southern Runner (Table 5-3). The parent 97-8-4 had the highest count of Cp lesions at 120 DAP but was not significantly different from Southern Runner. Significant differences among genotypes for lesion number per 10 leaves were reported in field tests for Ca (45). However

Table 5-1. Analysis of variance for square root transformed lesion counts per leaf for early leaf spot (Ca) and late leaf spot (Cp) across dates on the F_2 generation in Gainesville, Florida, 1996.

Source	df	Mean square	
		Ca	Cp
Reps	1	49.91*[1]	22.07ns
Entries[2]	15	14.56ns	29.42ns
Dates	1	35.39*	312.08**
Entry x Date	15	7.00ns	37.69ns

[1]*, **, and ***, Represent significance at the $P \leq 0.05$, 0.01, and 0.001 levels, respectively.
[2]Represents cross or parent.

Table 5-2. Analysis of variance for square root transformed lesion counts per 10 leaves for early leaf spot (Ca) and late leaf (Cp) spot on the F_2 generation in Gainesville, Florida, 1996.

Source	df	Mean square			
		Ca		Cp	
		120 DAP	145 DAP	120 DAP	145 DAP
Reps	1	59.33*[1]	22.06*	429.74**	214.8**
Genotype	15	16.40ns	5.48ns	59.88**	6.42ns

[1]*, **, and ***, Represent significance at the $P \leq 0.05$, 0.01, and 0.001 levels, respectively.

Table 5-3. Means for lesion counts per leaf for early leaf spot (Ca) and late leaf spot (Cp) on the F_2 generation in Gainesville, 1996.

	Ca		Cp	
Genotype	120 DAP	145 DAP	120 DAP	145 DAP
148/7/25 x S. Runner	44.1	47.0	28.2ef[1]	29.5
S. Runner	34.9	47.0	30.3a-d	32.0
S. Runner x 97-8-4	30.2	42.8	15.4c-e	35.0
Flamingo x S. Runner	29.9	41.2	14.1f	35.3
97-8-4 x 148/7/25	24.0	40.4	17.4c-f	40.4
Flamingo x 148/7/25	27.9	38.8	13.9c-f	22.8
97-8-4 x S. Runner	53.4	37.6	26.9a-e	47.1
148/7/25 x 97-8-4	43.2	38.0	31.3a-d	40.4
Flamingo	38.8	35.7	16.9f	40.4
S. Runner x 148/7/25	25.9	32.4	16.6cde	40.0
Flamingo x 97-8-4	28.6	34.2	36.1abc	34.2
97-8-4 x Flamingo	31.0	33.4	16.9c-f	40.4
148/7/25 x Flamingo	49.3	30.3	64.0def	40.0
S. Runner x Flamingo	31.0	27.9	52.0ab	29.2
148/7/25	14.9	26.2	12.1c-f	27.5
97-8-4	16.9	27.6	62.5a	31.0
Mean	31.0	36.1	19.9	34.6
Significance of F.	ns[2]	ns	**	ns

[1]Means followed by the same letter are not significantly different at the $P \leq 0.05$ level.
[2]*, **, and ***, represent significance at the $P \leq 0.05$, 0.01, and 0.001 levels, respectively.

lesion counts per leaf have been shown to be an unreliable component for evaluating peanut genotypes for resistance to leaf spot diseases (7, 14, 100). Further tests would be necessary to establish whether the differences in resistance to Cp among entries that were noted are repeatable. Although there were no significant differences among entries for lesion count for Ca, lesion count could be an important component of rate reducing resistance since total visual disease is a product of LC and lesion area. Environmental factors influence the total number of lesions that develop.

On both sampling dates, the mean lesion counts for Ca were higher than those for Cp (Table 5-3). However, the Cp lesion count increased from a mean of 19.9 lesion per leaf at 120 DAP to 34.6 at 145 DAP. This represents a 74% increase in lesion number for Cp compared to a 16% increase over the same period for Ca. The number of Cp lesions increased faster than Ca over the same period. This agrees with observations by Hemingway (51) that Cp disease increases faster and is more devastating than Ca. In Florida, Jackson (62) found that Cp predominated, but some fields had more Ca than Cp.

There was no correlation ($P>0.05$) in the numbers of Ca and Cp lesions at both sampling dates ($|r|= 0.039$ to 0.008). This supports the conclusion that inheritance of resistance to Ca and Cp are independent (4, 54). Other work however indicated that inheritance of resistance to the two pathogens in some populations is not independent (3).

Components and Plant Appearance Score

Results of correlation analysis between plant appearance scores and components of resistance are shown in Table 5-4. Plant appearance score was correlated with LP, SP, and TMPSL ($P \leq 0.05$) in the Florida test at 145 DAP but not at 120 DAP (Table 5-4). Correlations were low to moderate $0.070 \geq r \geq 0.537$. Amount of sporulation was the most highly correlated with PAS in the Florida tests, $r=0.537$ (Table 5-4). In Zimbabwe, LP and LD were significantly correlated with plant appearance score ($P \leq 0.05$) and correlations were low, $r=-0.360$ and 0.297 respectively. Plant appearance score was not correlated with SP and TMPSL ($P>0.05$) $r=0.005$ and 0.042 respectively. This may be due to differences in the leaf spot disease profiles. In Zimbabwe, web blotch caused by *Phoma arachidicola*, contributes significantly to defoliation and plant appearance score in addition to Ca and Cp. Defoliation is a major criterion included in the separation of categories in the plant appearance score rating scales.

In Florida, the main pathogens causing leaf spot diseases are Ca and Cp. Lesion diameter was not correlated with plant appearance scores on either date in the F_2 test in Florida.

The PAS1 values were not correlated with any of the components of resistance in Florida. At 120 DAP, disease intensity was at such a level that genotypic differences in resistance to Ca were not clearly expressed based on plant appearance score. As the season advanced, however, genotypic

Table 5-4. Correlations between components of resistance to early leaf spot and plant appearance scores determined at 120 (PAS1) and 145 days after planting (PAS2) on the F_2 generation in Gainesville, Florida, 1996.

Component[1]	PAS1	PAS2
LP	-0.277ns[2]	-0.516**
LD	-0.269ns	0.219ns
SP	0.142ns	0.537**
TMPSL	0.070ns	0.407*

[1]LP=latent period in days, LD=lesion diameter in mm, SP=sporulation score on a 1-5 scale, TMPSL=square root transformed percentage sporulating lesions.
[2]*, **, and ***, represent significantly different from zero at the $P \leq 0.05$, 0.01, and 0.001 levels, respectively.

differences in resistance showed more clearly. Genotypes with longer LP had reduced levels of disease at 145 DAP.

In Florida, SP was positively correlated with PAS2, thus genotypes that had heavier sporulation ultimately had more disease at 145 DAP. Plant appearance score is therefore a reliable and quick way to separate out resistant genotypes under field conditions. Plant appearance score was significantly correlated with more components of resistance in Florida than in Zimbabwe.

In Florida, TMPSL and SP were positively correlated with PAS2 (Table 5-4). Genotypes that had a higher percentage of lesions that were sporulating, had higher levels of disease at 145 DAP. Similar results were reported for Cp by Aquino et al. (6). Although lesion diameter was not correlated with plant appearance scores in Florida, it is an important component of resistance, since total disease is a function of lesion size and necrotic area per lesion. In general, the results agree with those reported by Waliyar et al. (135) who found that field score ratings for Ca were significantly correlated with several components of resistance determined in the greenhouse.

Field and Greenhouse Correlations

The relationship between greenhouse and field F_1 measurements of components of resistance to Ca were determined using Kendall's tau β rank correlation analysis.

Greenhouse and field measurements of LP, LD, and SP, were significantly and positively correlated ($P \leq 0.05$) and the r values were 0.594, 0.380, and 0.577, respectively. Measurements of LP made in the greenhouse may be used to make preliminary selections for the field situation. No reports of correlations of greenhouse and field measurements of LP for Ca were found in the literature. Measurement of LP in the greenhouse is easier than in the field and larger numbers of genotypes can be evaluated in the greenhouse per unit of time and labor. Greenhouse and field measurements of maximum percentage sporulating lesions were not significantly correlated ($P>0.05$). Measurements of MPSL in the greenhouse may not predict performance under field conditions. The correlation of greenhouse and field ratings of SP means that greenhouse measurements of SP may be used for preliminary screening of genotypes for spore production. Green and Wynne (45) reported significant correlations between greenhouse and field rating for sporulation of Ca.

Although greenhouse and field measurements for LD were correlated, the r value was low, ($r=0.380$). Selection for small lesion diameter would not be a reliable predictor of performance in the field.

Correlation of Components Within Tests

The associations among components of resistance within tests are presented in Table 5-8 to 5-14. If components are

strongly and consistently associated, then selection for resistance using one component would be expected to improve the correlated components. It would be desirable to identify one component that is quick and easy to use if it is correlated with other components.

Latent period (LP) and spore production (SP)

Latent period was significantly correlated ($P \leq 0.001$) with SP (Table 5-5 to 5-7) in all tests except the F_2 tests in Zimbabwe (Table 5-6). The r values for the correlation between LP and SP ranged from $|r|=0.293$ (Table 5-7) to $|r|=0.665$ (Table 5-5). This means that genotypes that had longer latent periods also had reduced sporulation. It should be possible to select genotypes with reduced spore production by selecting for either longer latent periods or sporulation.

The variation in r values is probably due to genotype x environment interactions. In two F_2 tests conducted in Zimbabwe during the 1991/92 and 1992/93 seasons, there were no significant correlations between LP and SP. In the 1991/92 season, disease development was influenced by drought conditions. The longest LP and the widest range in mean LP in all tests (12 days) was noted during this season. The high temperature and low relative humidity experienced during the period of disease development may have influenced the association between latent period and spore production. Wilting of plants during part of the day was observed during the duration of data collection. These factors may have

Table 5-5. Correlations among four components of resistance to early leaf spot measured on the F_1 greenhouse test, 1995, and F_1, and F_2 field tests, 1996, Gainesville, Florida.

	Component[1]			
	LP	LD	SP	TMPSL
F_1 Greenhouse 1995				
LP	1.000	0.028ns[2]	-0.427***	-0.397***
LD		1.000	0.123ns	0.143ns
SP			1.000	0.697***
TMPSL				1.000
F_1 1996				
LP	1.000	0.020ns	-0.665**	-0.399***
LD		1.000	-0.103ns	-0.038ns
SP			1.000	0.794***
TMPSL				1.000
F2 1996				
LP	1.000	0.003ns	-0.582***	-0.513**
LD		1.000	-0.112ns	-0.110ns
TMPSL			1.000	0.871**
TMPSL				1.000

[1]LP=latent period in days, LD=lesion diameter in mm, SP=sporulation score on a 1-5 scale, TMPSL=square root transformed percentage sporulating lesions.
[2]*, **, and ***, represent significantly different from zero at the $P \leq 0.05$, 0.01, and 0.001 levels, respectively.

Table 5-6. Correlations among four components of resistance to early leaf spot measured on the F_2 field test, Zimbabwe, 1991/92 and 1992/93.

	Component[1]			
	LP	LD	SP	TMPSL
1991/92				
LP	1.000	-0.041ns[1]	-0.195ns	-0.018ns
LD		1.000	0.114ns	0.155ns
SP			1.000	0.500**
TMPSL				1.000
1992/93				
LP	1.000ns	0.016ns	0.063ns	-0.112ns
LD		1.000	-0.306ns	-0.358*
SP			1.000	0.533**
TMPSL				1.000

[1]LP=latent period in days, LD=lesion diameter in mm, SP=sporulation score on a 1-5 scale, TMPSL=square root transformed percentage sporulating lesions.
[2]*, **, and ***, Represent significantly different from zero at the $P \leq 0.05$, 0.01, and 0.001 levels, respectively.

the duration of data collection. These factors may have

Table 5-7. Correlations among four components of resistance to early leaf spot measured on the F_3 field tests in Zimbabwe, 1992/93 and 1993/94 seasons.

	Components[1]			
	LP	LD	SP	TMPSL
1992/93				
LP	1.000	0.421***	-0.293*	-0.251*
LD		1.000	-0.046ns	-0.206ns
SP			1.000	0.613***
TMPSL				1.000
1993/94				
LP	1.000	-0.284*	-0.468***	-0.335*
LD		1.000	-0.207ns	-0.360**
SP			1.000	0.824***
TMPSL				1.000

[1]LP=latent period in days, LD=lesion diameter in mm, SP=sporulation score on a 1-5 scale, TMPSL=square root transformed percentage sporulating lesions.
[2]*, **, and ***, Represent significantly different from zero at the $P \leq 0.05$, 0.01, and 0.001 levels, respectively.

resulted in the lack of correlation between LP and SP and between LP and TMPSL during the 1991/92 season. Alderman and Beute (2) found that spore production was reduced with decreasing lesion water potential. Waliyar et al. (133) found that incubation periods for Ca were reduced with increased temperature. They also noted that on some genotypes incubation period interacted with temperature but other genotypes had stable incubation periods across temperatures.

During the 1992/93 season, mean LP had the shortest range of 3.0 days (Table 3-8). This reduced variability in the range of LP which may have influenced the correlation between the two variables.

However, in spite of the environmental influences, SP and LP were highly and significantly correlated in most tests conducted. The association between LP and SP was found to be generally consistent over most environments. It is necessary to evaluate genotypes over multiple environments when selecting genotypes for resistance to Ca.

Latent period (LP) and transformed maximum percentage sporulating lesions (TMPSL)

Latent period and maximum percentage sporulating lesions were significantly correlated ($P \leq 0.05$) (Tables 5-5 to 5-7), except for the F_2 tests conducted in Zimbabwe during the 1991/92 and 1992/93 seasons (Table 5-6). In all cases, the correlations between LP and TMPSL were negative. The possible reasons for the lack of correlation between the two components

in these two tests have been discussed in the previous section. Correlations between LP and TMPSL were moderate, ranging from |r|=0.018 (Table 5-6) to |r|=0.513 (Table 5-5). This means that selection for longer latent period also identifies genotypes with reduced percentage sporulating lesions. Reduced percentage sporulating lesions means a reduced amount of total inoculum that is produced which could give rise to new infections.

The association between LP and TMPSL was noted in diverse environments, Florida and Zimbabwe. Although the r values varied with environment, the association between the two components was generally consistent. These results show the variation that can be expected in the associations among components of resistance in different environments.

Sporulation (SP) and transformed maximum percentage sporulating lesions (TMPSL)

Maximum percentage sporulating lesions was highly and significantly correlated with amount of spore production ($P \leq 0.001$) in all tests. (Table 5-5 to 5-7). These components were the most highly correlated in different environments (r=0.500 to 0.871). In all cases the r values were positive, indicating that genotypes with a high sporulation score also had higher maximum percentage of sporulating lesions. The high and consistent correlation between the two components means that it should be possible to select for low sporulation per lesion and reduced percentage sporulating lesions using

only one of the components. These two components together are central to the epidemic development of Ca on a peanut crop since they account for the total amount of inoculum produced after primary lesions have been produced.

The determination of percentage sporulating lesions requires more labor than amount of sporulation per lesion using the 1-5 scale. Amount of sporulation was also frequently correlated with LP and is probably a more precise component. Selecting for reduced sporulation using the 1-5 scale should identify genotypes with reduced maximum percentage sporulating lesions. These results are as expected since they essentially deal with the same component. Ricker et al. (100) found a significant correlation between maximum percentage sporulating lesions and amount of spores produced per lesion with latent period measured as time from inoculation to the first two lesions sporulating.

Lesion diameter (LD), and other components

Lesion diameter was significantly correlated with LP ($P \leq 0.05$) in two tests (Table 5-7). The r values were relatively low, $r=0.421$ and $r=-0.284$ (Table 5-7). The association between LP and LD was low and inconsistent across environments. Waliyar et al. (135) found no correlation between LD and incubation period, defined as the number of days from inoculation to the appearance of lesions. In their tests, some highly resistant genotypes which were among the lowest in spore production, with some of the longest

incubation periods were found to have large lesions. Lesion diameter did not identify genotypes with low sporulation and longer incubation periods. Little progress would be expected from selecting genotypes with reduced LD due to the low and inconsistent association between LD and LP.

Lesion diameter was correlated with percentage sporulating lesions in two tests, r=-0.358, (Table 5-6) and r=-0.360 (Table 5-7). This suggests that genotypes with large lesions may have reduced percentage sporulating lesions. The r values however were low and were significant in only two of the eight tests conducted over different years and seasons. Lesion diameter would not be a consistent predictor of maximum percentage sporulating lesions. In studies reported by Waliyar et al. (135), lesion diameter was not correlated with amount of sporulation. Some genotypes with large lesions were among the lowest in spore production. The partially resistant genotype, 148/7/25 generally had large lesions even though it had a longer LP, low SP, and MPSL. In general LD was poorly correlated with MPSL and SP.

Correlations of Components Measured in Different Environments

Results of correlation analysis of components measured in different environments are shown in Table 5-8.

Correlations between Zimbabwe tests

Measurements of components of resistance in F_3 tests over two seasons were significantly and positively correlated.

($P \leq 0.05$). This occurred despite the fact that there were significant genotype x year interactions. The correlations were moderate (r=0.409 to 0.667). Amount of spore production showed the highest correlations between the two seasons (r=0.667). In contrast, measurement of components of resistance in two different seasons for the F_2 in 1991/92 and 1992/93 were not significantly correlated ($P>0.05$). This was attributed to year effects, genotype x environment interaction and the effects of drought.

Correlations between Zimbabwe and Florida tests

Correlations between measurements of LP made in Florida and in Zimbabwe were significant ($P \leq 0.001$) for the F_1 test in 1990/91 (Zimbabwe) and the F_1 test in 1995 (Florida), and between the F_2 of 1991/92 (Zimbabwe) and the F_2 in Florida, (1996). The correlations between the LP values from the F_2 of 1992/93 (Zimbabwe) and the F_2 of 1996 (Florida) was not significant ($P \leq 0.05$). This was attributed to the large variation between the two seasons, as discussed previously.

The correlation between SP measurements in the F_2 test in 1991/92 (Zimbabwe) and F_2 in 1996 (Florida) was significant (r=0.406) ($P \leq 0.05$). This positive correlation may be due to the fact that mean temperatures during the 1991/92 season in Zimbabwe were comparable to those in Gainesville, Florida in 1996. No other tests were correlated for SP between the tests in Zimbabwe and Florida.

Table 5-8. Pearson's correlations between components of resistance measured in different environments 1990/91 to 1996 in Zimbabwe and in Florida.

Generations	Components[1] LP	LD	SP	TMPSL
F_1, Zimbabwe, 1990/91 and F_1 in Florida, 1996.	0.235ns[2]	0.059ns	0.093ns	ND[3]
F_1, Zimbabwe, 1990/91 and F_1, 1995, in Florida.	0.658**	0.065ns	0.336ns	ND
F_2, Zimbabwe, 1992/93 and F_2 in Florida, 1996.	0.155ns	0.253ns	0.033ns	0.385ns
F_2, Zimbabwe, 1991/92 and F_2 in Florida, 1996.	0.758**	-0.131ns	0.407*	0.121ns
F_2, Zimbabwe, 1991/92 and F_2 1992/93 in Zimbabwe.	0.277ns	0.038ns	0.040ns	0.324ns
F_3, Zimbabwe, 1992/93 and F_3 1993/94 in Zimbabwe.	0.450*	0.409*	0.667*	0.462**

[1]LP=latent period in days, LD=lesion diameter in mm, SP=sporulation score on a 1-5 scale, TMPSL=square root transformed percentage sporulating lesions.
[2]*, **, and ***, Represent significantly different from zero at the $P \leq 0.05$, 0.01, and 0.001 levels, respectively.
[3]ND=No data.

All other correlations of components measured in Zimbabwe and Florida were not significant ($P>0.05$). Overall, the correlations between measurements made in Zimbabwe and in Florida were not significantly different from zero for LD, SP, and TMPSL. The difference in environmental conditions may have influenced the correlations between measurements from the different sites. The lack of correlation could be attributed to differences in physiological races of Ca found in Zimbabwe and Florida. This may account for the variable reaction of resistant genotypes when tested in different environments reported by Waliyar et al. (135, 136) and Nigam et al. (92). Differences in physiological isolates of Ca collected from different countries have been demonstrated (Subba Rao et al., 126). It appears that the physiological mechanisms that lead to the effect of genotype on latent period may be independent of the prevalent physiological strain.

CHAPTER VI
SUMMARY AND CONCLUSIONS

This research was conducted to study the inheritance of resistance to early leaf spot in the cultivated peanut. Four components of rate reducing resistance, latent period (LP) lesion diameter (LD), amount of sporulation, (SP), and maximum percentage sporulating lesions (MPSL) were studied. The studies were carried out at two diverse locations in Florida and in Zimbabwe over six different seasons to examine the stability of components of resistance. The procedures used were analysis of variance, diallel combining ability analyses, regression analyses and correlations analyses on the components of resistance.

Significant differences were noted for all components of resistance in four or more tests for each component indicating that genetic variability exists. Selection for improved resistance using the different components should be possible. There were genotype x environment interactions for latent period and percentage sporulating lesions. It is necessary to evaluate genotypes in multiple environments in order to ensure reliability in breeding for resistance to early leaf spot, using components of partial resistance.

Narrow sense heritability estimates significantly different from zero were obtained indicating that the genotypic differences are heritable. Narrow sense heritability estimates ranged from low to high for the different components, 0.0 to 0.64 for LP, from 0.0 to 0.45 for LD, from 0.0 to 1.23 for SP, and from 0.0 to 1.20 for MPSL. Narrow sense heritability estimates were higher in Florida than in Zimbabwe. It may be essential to determine the estimates of heritability for components of resistance within a location before embarking on a long term breeding program using components of rate reducing resistance for early leaf spot.

Latent period and maximum percentage sporulating lesions were the most consistent components of resistance in evaluation of genotypes for resistance to early leaf spot. Although spore production was relatively consistent, it was influenced more by environmental variation than LP and MPSL. Lesion diameter was inconsistent in evaluating genotypes for resistance to early leaf spot.

General combining ability was significant in one or more tests for all components of resistance. Specific combining ability was significant for all components of resistance in at least one test, indicating that nonadditive genetic effects could also be important. The ratio of GCA/SCA for the components ranged from 5 to 11 for LP, 2 to 3 for LD, 4 to 21 for SP, and 3 to 6 for MPSL. Additive genetic effects were

more important than non additive effects in the control of partial resistance. Resistance to Ca is controlled largely by multiple genes with additive effects. Selection of individual plants from crosses, in early generations should be an effective procedure in breeding for resistance to Ca. Significant reciprocal effects were noted, indicating that cytoplasmic factors are probably involved in the control of resistance to Ca.

The parent, 148-7-25 was the best to use in developing resistance to early leaf spot and Southern Runner had the largest negative effect on levels of resistance among progeny.

Latent period was significantly and negatively correlated with amount of sporulation ($r=-0.251$ to -0.666). Amount of sporulation was significantly and positively correlated with maximum percentage sporulating lesions ($r=0.500$ to 0.824). This may mean that selection for one component may lead to improvement in other components. Lesion diameter was poorly correlated with other components and the relationship was inconsistent. When used alone therefore, LD may not be a useful predictor of LP, SP, and MPSL. Latent period was the best indicator of resistance to Ca based on the highly significant differences among entries noted in most environments. It is also highly correlated with most other components of resistance.

Correlations between measurements of components between Zimbabwe and Florida were generally low. This may indicate

differences in the early leaf spot pathogen populations between Zimbabwe and Florida. Genotypes that show resistance to Ca in Florida may not necessarily be useful against early leaf spot in Zimbabwe. However, weather/drought differences between Zimbabwe and Florida were probably a factor.

Components of resistance LP and MPSL were correlated with a field plant appearance score for rating plants for disease levels at harvest (Florida 1-10 scale) ($|r|=0.219$ to 0.516) in Florida. This indicates that plant appearance score can be a useful, quick and easy way to identify genotypes with high levels of components of partial resistance to leaf spot diseases.

APPENDIX A
GLOSSARY OF TERMS

Additive gene effects: gene action in which the effects of a genetic trait are enhanced by each additional gene, either an allele at the same locus, or genes at different loci. Additive genes contribute to the additive genetic variance.

Nonadditive gene effects: gene action with deviations from the additive model such that the heterozygote is more like one parent than the other.

General combining ability (GCA): the average or overall performance of a genetic strain in a series of crosses.

Heritability: a portion of the observed variance in the progeny that is inherited. This is what determines the degree of resemblance between relatives.

Narrow sense heritability: the proportion of the additive genetic variance to the total phenotypic variance.

Specific combining ability (SCA): the performance of specific combinations of genetic strains in crosses in relation to the average performance of all combinations.

APPENDIX B

SEASONAL RAINFALL AT GWEBI VARIETY TESTING CENTER, ZIMBABWE, NOVEMBER TO MAY FOR THE 1990/91, 1991/92, 1992/93 AND 1993/4 SEASONS AND AT GREEN ACRES RESEARCH FARM, GAINESVILLE, FLORIDA, MAY TO SEPTEMBER, 1996.

Gwebi Variety Testing Center, Zimbabwe

	Monthly Rainfall			
	1990/91	1991/92	1992/93	1993/94
	mm			
November	78.7	117.0	49.2	76.0
December	99.9	87.1	161.6	67.7
January	167.2	139.2	223.8	315.1
February	112.7	40.0	136.2	129.2
March	199.8	98.1	85.1	103.8
April	36.0	35.1	43.2	58.7
May	27.0	0.0	0.0	0.0
Total	723.5	516.5	699.10	750.5

Green Acres Research Farm, Gainesville, Florida, 1996

Month	Rainfall (mm)
May	39.0
June	168.5
July	213.5
August	227.5
September	46.8
Total	695.3

APPENDIX C

MAXIMUM, MINIMUM, AND MEAN DAILY TEMPERATURE IN THE GREENHOUSE IN GAINESVILLE, FLORIDA, 16 JULY TO 23 SEPTEMBER, 1995.

	July			August			September		
				°C					
Date	Min	Max	Mean	Min	Max	Mean	Min	Max	Mean
1				26	49	37.5	24	42	33.0
2				21	49	35.0	23	44	33.5
3				26	35	30.5	23	44	33.5
4				26	50	35.5	22	44	33.0
5				26	50	38.0	22	42	32.0
6				26	49	38.0	24	35	29.5
7				27	49	38.0	25	42	33.5
8				27	49	38.0	22	42	32.0
9				26	49	37.5	21	45	33.0
10				26	49	37.5	21	44	32.5
11				26	49	36.5	22	45	33.5
12				26	47	36.5	22	44	33.0
13				26	49	37.5	21	44	32.5
14				27	50	68.5	21	44	32.5
15				29	49	39.0	22	43	32.5
16	21	48	34.5	26	51	38.5	23	45	34.0
17	25	50	37.5	28	49	38.5	25	45	35.0
18	30	37	33.5	29	49	39.0	24	44	34.0
19	32	46	39.0	28	50	39.0	23	44	33.5
20	22	45	33.5	27	48	37.5			
21	28	36	32.0	26	49	37.5			
22	28	53	40.5	23	44	35.5			
23	23	42	32.5	22	45	33.6			
24	22	45	33.5	26	45	33.6			
25	27	50	38.5	26	45	35.5			
26	21	51	36.0	26	47	35.5			
27	26	51	38.5	28	47	35.5			
28	25	51	38.0	27	46	37.5			
29	21	49	35.0	27	46	36.5			
30	28	47	37.5	26	47	36.5			
31	26	50	38.0	27	46	37.0			

APPENDIX D

ESTIMATES OF SPECIFIC COMBINING ABILITY (SCA) EFFECTS FOR COMPONENTS OF RESISTANCE TO EARLY LEAF SPOT, MEASURED ON THE F_1 GENERATION IN GAINESVILLE, FLORIDA, 1995.

Female		Male parent			
	Component[1]	S. Runner	Flamingo	97-8-4	148-7-25
S. Runner	LP	-	0.86	-0.45	-0.32
	LD	-	0.08	0.09	0.02
	SP	-	0.19	0.08	0.06
	TMPSL	-	0.34	-0.13	0.03
Flamingo	LP	-0.07	-	-0.94	-0.27
	LD	-0.11	-	0.12	0.14
	SP	0.11	-	-0.06	-0.10
	TMPSL	0.54	-	0.06	-0.35
97-8-4	LP	-0.83	-0.70	-	0.14
	LD	0.40	-0.29	-	0.15
	SP	0.22	-0.10	-	0.19
	TMPSL	0.57	-0.09	-	0.15
148-7-25	LP	0.44	0.28	0.09	-
	LD	0.08	0.29	0.09	-
	SP	0.00	0.01	0.06	-
	TMPSL	-0.52	-0.15	0.48	-

S.E.	s_{ij}[2]	S.E.	r_{ij}[3]
LP	$\pm$ 0.72	LP	$\pm$ 1.07
LD	$\pm$ 0.19	LD	$\pm$ 0.24
SP	$\pm$ 0.19	SP	$\pm$ 0.24
TMPSL	$\pm$ 0.55	TMPSL	$\pm$ 0.70

[1]LP=measurement in days, Ld=measurement in mm, SP=spore production score on a 1-5 scale.
[2]Standard error of SCA effects for crosses.
[3]Standard error of SCA effects for reciprocals.

APPENDIX E

ESTIMATES OF SPECIFIC COMBINING ABILITY (SCA) EFFECTS FOR COMPONENTS OF RESISTANCE TO EARLY LEAF SPOT, MEASURED IN THE FIELD ON THE F_2 GENERATION IN GAINESVILLE, FLORIDA, 1996.

Female	Component[1]	Male parent			
		S. Runner	Flamingo	97-8-4	148-7-25
S. Runner	LP	-	-0.06	-0.30	-0.32
	LD	-	-0.18	0.17	-0.07
	SP	-	0.16	-0.03	-0.11
	TMPSL	-	0.35	0.52	0.00
Flamingo.	LP	0.63	-	-0.47	-0.05
	LD	0.19	-	0.19	-0.01
	SP	0.13	-	0.04	0.04
	TMPSL	0.62	-	0.14	-0.07
97-8-4	LP	0.29	-0.39	-	-0.91
	LD	0.01	-0.27	-	-0.12
	SP	0.23	-0.06	-	-0.04
	TMPSL	0.47	-0.18	-	-0.22
148-7-25	LP	1.20	0.81	-0.23	-
	LD	0.15	0.13	-0.14	-
	SP	-0.09	0.00	-0.18	-
	TMPSL	-0.01	0.25	-0.25	-

S.E.	s_{ij}[2]	S.E.	r_{ij}[3]
LP	± 0.51	LP	± 0.65
LD	± 0.08	LD	± 0.31
SP	± 0.16	SP	± 0.63
TMPSL	± 0.65	TMPSL	± 0.51

[1]LP=measurement in days, LD=measurement in mm, SP=spore production score on a 1-5 scale, TMPSL=square root transformed maximum percentage sporulating lesions.
[2]Standard error of SCA effects for crosses.
[3]Standard error of SCA effects for reciprocals.

APPENDIX F

ESTIMATES OF SPECIFIC COMBINING ABILITY (SCA) EFFECTS FOR COMPONENTS OF RESISTANCE TO EARLY LEAF SPOT, MEASURED ON THE F_1 GENERATION AT GWEBI, ZIMBABWE, 1990/91.

Female		Male parent			
	Component[1]	S. Runner	Flamingo	97-8-4	148-7-25
S. Runner	LP	-	0.64[2]	-0.65	0.44
	LD	-	0.22	-0.12	0.12
	SP	-	-0.02	-0.09	0.28
	TMPSL	-	-	-	-
Flamingo	LP	-2.34	-	-1.13	0.42
	LD	0.26	-	-0.08	-0.06
	SP	0.07	-	0.09	-0.07
	TMPSL	-	-	-	-
97-8-4	LP	2.03	0.78	-	0.12
	LD	0.08	0.26	-	-0.07
	SP	0.17	-0.14	-	-
	TMPSL	-	-	-	-
148-7-25	LP	3.65	1.45	1.95	-
	LD	-0.08	-0.20	-0.10	-
	SP	-0.60	-0.06	-0.08	-
	TMPSL	-	-	-	-

S.E.	s_{ij}[3]	S.E.	r_{ij}[4]
LP	$\pm$ 2.14	LP	$\pm$ 2.72
LD	$\pm$ 0.32	LD	$\pm$ 0.41
SP	$\pm$ 0.20	SP	$\pm$ 0.25

[1]LP=latent period in days, LD=lesion diameter in mm, SP=sporulation score on a 1-5 scale, TMPSL=square root transformed maximum percentage sporulating lesions.
[2]Values are not significantly different from zero.
[3]Standard error of SCA effects for crosses.
[4]Standard error of SCA effects for reciprocals.

APPENDIX G

ESTIMATES OF SPECIFIC COMBINING ABILITY (SCA) EFFECTS FOR COMPONENTS OF RESISTANCE TO EARLY LEAF SPOT, MEASURED ON THE F_2 GENERATION AT GWEBI, ZIMBABWE, 1991/92.

Female		Male parent			
	Component[1]	S. Runner	Flamingo	97-8-4	148-7-25
S. Runner	LP	-	1.11	-1.20	-0.76
	LD	-	-0.16	-0.01	0.13
	SP	-	-0.07	-0.02	-0.07
	TMPSL	-	0.09	-0.91	0.41
Flamingo	LP	-0.18	-	0.76	0.42
	LD	0.02	-	0.21	0.01
	SP	0.26	-	0.16	0.08
	TMPSL	0.32	-	0.80	-0.55
97-8-4	LP	3.08	-1.60	-	-0.52
	LD	0.04	0.03	-	0.09
	SP	0.29	0.26	-	0.02
	TMPSL	-0.04	0.00	-	0.59
148-7-25	LP	4.90	-0.56	0.92	-
	LD	0.00	-0.25	0.02	-
	SP	0.05	-0.26	-0.13	-
	TMPSL	-0.17	-0.63	1.48	-

S.E.	s_{ij}[3]	S.E.	r_{ij}[4]
LP	± 1.99	LP	± 2.52
LD	± 0.22	LD	± 0.28
SP	± 0.23	SP	± 0.29
TMPSL	± 0.56	TMPSL	± 0.71

[1]LP=measurement in days, LD=measurement in mm, SP=sporulation score on a 1-5 scale, TMPSL=square root transformed maximum percentage sporulating lesions.
[2]Values were not significantly different from zero.
[3]Standard error of SCA effects for crosses.
[4]Standard error of SCA effects for reciprocals.

APPENDIX H

ESTIMATES OF SPECIFIC COMBINING ABILITY (SCA) EFFECTS FOR COMPONENTS OF RESISTANCE TO EARLY LEAF SPOT, MEASURED ON THE F_2 GENERATION AT GWEBI, ZIMBABWE, 1992/93.

Female		Male Parent			
	Component[1]	S. Runner	Flamingo	97-8-4	148-7-25
S. Runner	LP	-	-0.20	1.59	-1.15
	LD	-	0.35	0.04	0.43
	SP	-	-0.14	-0.08	0.26
	TMPSL	-	-0.66	-0.39	0.61
Flamingo	LP		-	-0.13	1.05
	LD		-	-0.09	0.02
	SP		-	0.13	0.17
	TMPSL		-	0.15	0.05
97-8-4	LP			-	0.04
	LD			-	0.33
	SP			-	0.13
	TMPSL			-	-0.16
148-7-25	LP				-
	LD				-
	SP				-
	TMPSL				-

S.E.	s_{ij}[2]
LP	$\pm$ 0.53
LD	$\pm$ 0.23
SP	$\pm$ 0.21
TMPSL	$\pm$ 0.47

[1]LP=measurement in days, LD=measurement in mm, SP=sporulation score on a 1-5 scale, TMPSL=square root transformed maximum percentage sporulating lesions.
[2]Values are not significantly different from zero (P>0.05).
[3]Standard error of SCA effects for crosses.

APPENDIX I

ESTIMATES OF GENERAL COMBINING ABILITY (GCA) FOR COMPONENTS OF RESISTANCE TO EARLY LEAF SPOT, MEASURED ON THE F_3 GENERATION, AT GWEBI, ZIMBABWE, 1992/93 AND 1993/94.

Parent	Component[1]			
	LP	LD	SP	TMPSL
	Zimbabwe, 1992/93			
S. Runner	-1.07[2]	-0.10	0.04	0.04
Flamingo	0.24	0.09	-0.03	-0.03
97-8-4	0.47	-0.04	0.00	0.00
148-7-25	0.36	0.05	-0.01	0.01
S E ± =	0.38	0.06	0.04	0.22
	Zimbabwe, 1993/94			
S. Runner	-0.64	-0.15	0.29	0.30
Flamingo	0.34	0.03	-0.10	0.03
97-8-4	0.59	0.08	-0.12	-0.24
148-7-25	-0.29	0.19	-0.07	-0.03
S E ± =	0.74	0.32	0.23	0.32

[1]LP=latent period in days, LD=lesion diameter in mm, SP=sporulation score on a 1-5 scale, TMPSL=square root transformed maximum percentage sporulating lesions.
[2]Values were not significantly different from zero (P>0.05).

APPENDIX J

ESTIMATES OF SPECIFIC COMBINING ABILITY (SCA) EFFECTS FOR COMPONENTS OF RESISTANCE TO EARLY LEAF SPOT, MEASURED ON THE F_3 GENERATION AT GWEBI, ZIMBABWE, 1992/93.

Female		Male parent			
	Component[1]	S. Runner	Flamingo	97-8-4	148-7-25
S. Runner	LP	-	0.08[2]	0.39	0.34
	LD	-	-0.05	-0.09	0.09
	SP	-	-0.01	-0.07	0.05
	TMPSL	-	0.01	-0.14	0.06
Flamingo	LP	-0.03	-	0.17	-0.56
	LD	-0.12	-	-0.02	-0.11
	SP	0.01	-	0.00	-0.05
	TMPSL	0.60	-	0.03	0.08
97-8-4	LP	2.00	0.27	-	0.28
	LD	0.12	0.05	-	0.00
	SP	-0.03	0.03	-	0.01
	TMPSL	0.13	0.06	-	-0.05
148-7-25	LP	0.89	0.30	-0.17	-
	LD	0.12	0.07	0.02	-
	SP	-0.08	-0.07	0.01	-
	TMPSL	-0.54	-0.74	-1.00	-

S.E.	s_{ij}[3]	S.E.	r_{ij}[4]
LP	$\pm$ 0.50	LP	$\pm$ 0.63
LD	$\pm$ 0.11	LD	$\pm$ 0.45
SP	$\pm$ 0.06	SP	$\pm$ 0.08
TMPSL	$\pm$ 0.40	TMPSL	$\pm$ 0.51

[1]LP=measurement in days, LD=measurement in mm, SP=sporulation score on a 1-5 scale, TMPSL=square root transformed maximum percentage sporulating lesions.
[2]Values were not significantly different from zero (P>0.05).
[3]Standard error of SCA effects for crosses.
[4]Standard error of SCA effects for reciprocals.

APPENDIX K

ESTIMATES OF SPECIFIC COMBINING ABILITY (SCA) EFFECTS FOR COMPONENTS OF RESISTANCE TO EARLY LEAF SPOT, MEASURED ON THE F_3 GENERATION AT GWEBI, ZIMBABWE, 1993/94.

Female		Male Parent			
	Component[1]	S. Runner	Flamingo	97-8-4	148-7-25
S. Runner	LP	-	1.44[1]	0.95	-1.08
	LD	-	-0.14	-0.14	-0.23
	SP	-	-0.26	-0.20	0.73
	TMPSL	-	-0.10	-0.24	-0.51
Flamingo	LP	-	-	-1.21	-0.51
	LD		-	0.22	0.26
	SP		-	-0.06	-0.02
	TMPSL		-	-0.30	0.37
97-8-4	LP			-	1.22
	LD			-	-0.28
	SP			-	-0.07
	TMPSL			-	-0.45
148-7-25	LP				-
	LD				-
	SP				-
	TMPSL				-

S.E.	s_{ij}[3]
LP	± 0.74
LD	± 0.21
SP	± 0.23
TMPSL	± 0.54

[1]LP=measurement in days, LD=measurement in mm, SP=sporulation score on a 1-5 scale, TMPSL=square root transformed maximum percentage sporulating lesions.
[2]Values were not significantly different from zero (P>0.05).
[3]Standard error of SCA effects for crosses.

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BIOGRAPHICAL SKETCH

Zwenhamo A. Chiteka was born on July 18, 1954, in Makoni district, Zimbabwe. He attended secondary school from 1969 to 1972 at Nyanga Secondary School in Zimbabwe and then studied advanced levels and obtained the Cambridge Higher School Certificate in mathematics, physics, and chemistry. He enrolled for a B. Sc. (agriculture with honors) degree at the University of Zimbabwe in 1976 and successfully completed the program with a major in crop science in 1978. He served as lecturer in agronomy at Chibero College of Agriculture in Zimbabwe from 1979 to 1982. He was then appointed Research officer (peanut breeder) in the Crop Breeding Institute of the Department of Research and Specialist Services in the Ministry of Agriculture, Zimbabwe in 1982. In 1983 he attended a three month course in peanut improvement at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) in Hyderabad, India. He was awarded a USAID scholarship to study for the degree of Master of Science in agronomy at the University of Florida in August 1985 and completed in 1987. Mr. Chiteka then returned to Zimbabwe and continued to serve as principal research officer (peanut breeder) in the Crop Breeding Institute. During this period, Mr Chiteka served as interim potato breeder, 1990 to 1992, and served as the acting

head of the Crop Breeding Institute on various occasions. Mr Chiteka was awarded a Rockefeller Foundation Fellowship in 1990 to study for the degree of Ph. D. at the University of Florida. In 1994, Mr Chiteka was appointed to the position of lecturer (plant breeding and genetics) in the Department of Crop Science, University of Zimbabwe, and later enrolled for the Doctor of Philosophy degree at the University of Florida during the fall of 1994. Zwenhamo is married to Juliana, the last daughter of Mr. and Mrs. R. Museka, and they have six children, Tafadzwa Francis, Nyaradai Flavian, Wadzanai Maria Rosa, Hazvirehwi Theresa, Tariro Rosewinter, and Fidelis Blessing.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Daniel W. Gorbet, Chair
Professor of Agronomy

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David S. Wofford, Cochair
Associate Professor of
Agronomy

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Kenneth J. Boote
Professor of Agronomy

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Frederick M. Shokes
Professor of Plant
Pathology

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This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate School and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

May, 1997

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